Traveling waves in a coupled reaction-diffusion and difference model of hematopoiesis

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Abstract

The formation and development of blood cells is a very complex process, called hematopoiesis. This process involves a small population of cells called hematopoietic stem cells (HSCs). The HSCs are undifferentiated cells, located in the bone marrow before they become mature blood cells and enter the blood stream. They have a unique ability to produce either similar cells (self-renewal), or cells engaged in one of different lineages of blood cells: red blood cells, white cells and platelets (differentiation). The HSCs can be either in a proliferating or in a quiescent phase. In this paper, we distinguish between dividing cells that enter directly to the quiescent phase and dividing cells that return to the proliferating phase to divide again. We propose a mathematical model describing the dynamics of HSC population, taking into account their spatial distribution. The resulting model is an age-structured reaction-diffusion system. The method of characteristics reduces this model to a coupled reaction-diffusion equation and difference equation with delay. We study the existence of traveling wave fronts connecting the zero steady state with the unique positive uniform one. We use a monotone iteration technique coupled with the upper and lower solutions method.

Keywords: Hematopoiesis; Traveling wave front; Age-structured population; Reaction-diffusion system with delay; Difference equation
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1. Introduction

Hematopoiesis is the process that leads to the production and regulation of blood cells. It can be defined as a set of mechanisms that ensure the continuous and controlled replacement of the various blood cells. All blood cells arise from a common origin in the bone marrow, the hematopoietic stem cells (HSCs). These stem cells are undifferentiated and have a high proliferative potential. They can proliferate and mature to form all types of blood cells: the red blood cells, white cells and platelets. They have abilities to produce by division either similar cells with the same maturity level (self-renewal), or cells committed to one of the three blood cell types (differentiation) (see [39]). The HSCs compartment is separated in two sub-compartments: proliferating and quiescent (nonproliferating or resting). Quiescent cells represent the major part of HSC population (90% of HSCs are in quiescent phase, also called G_0-phase, [41]). Proliferating cells are actually in the cell cycle where they are committed to divide during mitosis at the end of this phase. After division, the two newborn daughter cells, either enter directly into the quiescent phase (long-term proliferation), or return immediately to the proliferating phase to divide again (short-term proliferation), [2, 19, 36]. More details about HSC dynamics can be found, *e.g.* in [21]. We will take here into account spatial cell distribution inside the bone marrow.

It is believed that several hematological diseases are due to some abnormalities in the feedback loops between different compartments of hematopoietic stem cell populations. Among a wide variety of disorders affecting blood cells, myeloproliferative diseases are of great interest. They are characterized by a group of conditions that cause blood cells to grow abnormally. They include chronic myelogenous leukemia, a cancer of white blood cells. Myeloproliferative disorders usually originate from the HSC compartment: an uncontrolled proliferation in the HSC compartment can perturb the entire system and leads to a quick proliferation. The excessive proliferation of malignant HSCs changes normal cell distribution in the bone marrow. If the proliferation of malignant HSCs is sufficiently fast, then the disease can invade the whole bone marrow. The propagation of malignant HSCs may correspond to traveling wave fronts of a reaction-diffusion equation.

The first mathematical model of HSC dynamics has been introduced in 1978 by Mackey, [24], inspired by works of Burns and Tannock, [15]. Mackey proposed a system of two uncoupled delay differential equations to describe the dynamics of HSC populations, and applied his model to a blood disease, aplastic anemia. The delay describes the average cell cycle duration. The model of Mackey stressed the influence of some factors such as the apoptotic rate, the introduction rate, the cell cycle duration, playing an important role in the appearance of periodic solutions. Since then, Mackey's model has been improved by many authors, including Mackey and co-authors, [8, 9, 10, 25, 26, 29, 30], Adimy and co-authors, [1, 2, 3, 4, 5, 6], and the references therein.

Traveling wave fronts have been widely studied for reaction-diffusion equations modeling a variety of biological phenomena (see for instance, [13, 20, 31, 37] and the references therein), and for time-delayed reaction-diffusion equations (see [12, 35, 38, 42, 43]). In [23], the authors considered a HSC dynamics model that took into account spatial diffusion of cells. The investigators have simply added a diffusion term to the corresponding delay differential equation. But in recent years it has become recognized that there are modeling difficulties with this approach (see [11, 32]). The problem is that individuals have not been at the same point in space at previous times. To attempt to address this difficulty, we use a general principle by which certain retarded differential equations can be obtained from age-structured population models or renewal equations (see [11, 32, 38]).

The investigations of asymptotic speeds of spread for biological systems are attracting more and more attention (see, *e.g.*, [7, 16, 18, 22, 34, 35, 45] and references therein). The concept of asymptotic speeds of spread was first introduced by Aronson and Weinberger [7] for reaction-diffusion equations. It was extended to a large class of integral equations by Diekmann [16], Thieme [34] and Thieme and Zhao [35]. Some mathematical tools were developed to make the link between the traveling wave solutions and the spreading speeds for reaction-diffusion equations with delays, such as integral equation approach by Thieme and Zhao [35], and monotone semiflows method by Liang and Zhao [22] and Fang and Zhao [17] (see also [18]).

In this paper, based on the model of Mackey, [24], we propose a more general system of HSC dynamics. As in [24], we take into account the fact that a cell cycle has two phases, that is, HSCs are either in a quiescent phase or actively proliferating. However, we do not suppose that after each division necessarily the two daughter cells enter the quiescent phase. We suppose that only a fraction of daughter cells enters the quiescent phase (long-term proliferation) and the other fraction of cells returns immediately to the proliferating phase to divide again (short-term proliferation), [33]. We also take into account the spatial diffusion of cells in the bone marrow. We obtain a system of two age-structured reaction-diffusion equations. By integrating the system over the age and using the characteristics method, we reduce it to a reaction-diffusion equation with time delay and nonlocal terms coupled with a continuous difference equation with nonlocal properties as well, that is the system (8). Despite the fact that the system (8) generates a monotone semiflow, the method developed by Liang and Zhao [22] cannot be applied to (8). This is because the solution map Q_t associated with the reaction-diffusion and difference system (8) on the space $X \times C([-r,0],X)$, where $X = BUC(\mathbb{R},\mathbb{R})$ is the Banach space of all bounded and uniformly continuous functions from $\mathbb{R}$ to $\mathbb{R}$ and $r > 0$ is the time delay, is not compact for $t > 0$ with respect to compact open topology. This can be seen from a very simple example. Indeed, if we consider the semigroup P_t generated by the difference equation $u(t) = \mu u(t-r)$, with $\mu = 2Ke^{-\gamma r} \in (0,1)$, on the space $\overline{C} := \{u_0 \in C([-r,0],\mathbb{R}) : \ u_0(0) = \mu u_0(-r)\}$, we obtain, for $\theta \in [-r,0]$ and $t \geq 0$, $P_t(u_0)(\theta) = P_{t+\theta}(u_0)(0)$ if $t+\theta \geq 0$ and $P_t(u_0)(\theta) = u_0(t+\theta)$ if $t+\theta \leq 0$. So, if we fix $t > 0$ and consider the positive integer n such that $(n-1)r \leq t < nr$, we get $P_t(u_0)(\theta) = \mu^n u_0(t+\theta-nr)$, for $(n-1)r - t \leq \theta \leq 0$ and $P_t(u_0)(\theta) = \mu^{n-1}u_0(t+\theta-(n-1)r)$, for $-r \leq \theta \leq (n-1)r - t$. Then, $\sup_{-r\leq\theta\leq 0}|P_t(u_0)(\theta)| = \mu^{n-1}\max\{\sup_{t-nr\leq s\leq 0}|u_0(s)|, \mu\sup_{-r\leq s\leq t-nr}|u_0(s)|\}$. Furthermore, if we consider the set $\mathcal{U} = \{u_0 \in \overline{B}_\mu : \sup_{t-nr\leq s\leq 0}|u_0(s)| = \mu\}$, where $\overline{B}_\mu$ is the closed ball of radius μ in the space $\overline{C}$, we obtain $P_t(\mathcal{U}) = \{u_0 \in \overline{B}_\mu : \sup_{-r\leq s\leq (n-1)r-t}|u_0(s)| = \mu^n\}$. Then, by the Riesz's theorem, $P_t(\mathcal{U})$ is not a compact set of $\overline{C}$. The compactness property of the solution map plays an important role in the method of Liang and Zhao [22] since in the proof of the existence of traveling waves, one needs to construct various sequences of functions and pass in them to limits to obtain a traveling wave. Later on, Fang and Zhao [17] extended the results of Liang and Zhao [22] to monotone semiflows with weak compactness "point-α-contraction". We can also show that the semigroup P_t defined above, is not compact in the sense of "point-α-contraction", for $0 < t < r$. We use the Kuratowski measure of noncompactness in $\overline{C}$ (see, *e.g.* [17]), which is defined by $\alpha(B) := \inf\{\zeta > 0 : B \text{ has a finite cover of diameter } < \zeta\}$, for any bounded set B of $\overline{C}$. Then, $\alpha(P_t(\mathcal{U})) = \mu^{n-1}\alpha(\mathcal{U})$. If we choose $0 < t < r$ $(n = 1)$, we obtain $\alpha(P_t(\mathcal{U})) = \alpha(\mathcal{U})$. So, P_t is not compact in the sense of "point-α-contraction", for $0 < t < r$. We also would like to mention that the system (8) cannot be reduced to an integral equation such that the theory developed by Thieme and Zhao [35] can be applied.

Our propose is to study monotone traveling waves for the coupled reaction-diffusion and difference system (8) by reducing the problem to the existence of an admissible pair of upper and lower solutions, and by using a monotone iteration technique. Using this approach, we obtain the existence of monotone traveling waves for $c \geq c^\star$ and nonexistence of traveling waves for

$c < c^\star$. We also show that $c^\star$ is the minimum wave speed for monotone traveling waves. It seems that using the monotone iteration technique provides some additional information about the solution, *e.g.* an approximate shape of the traveling wave profiles.

The organization of the paper is as follows. In Section 2, we describe the biological background leading to an age-structured reaction-diffusion model of HSC dynamics. In Section 3, by using the method of characteristics, we reduce this system to a coupled reaction-diffusion equation and difference equation with delay. In Section 4, we study the existence, uniqueness and positivity of the solutions by a comparison principle for upper and lower solutions. In Section 5, we present our main results. It is the study devoted to the existence of traveling wave fronts by using a method based on the notion of upper and lower solutions. In Section 6, we give some numerical simulations for traveling wave fronts. To end this section, we discuss the problem of existence of asymptotic speeds of spread for the system (8). In particular, we prove that the solution (N, u) of (8) satisfies $\lim_{t\to+\infty,\, |x|\geq ct}(N, u) = (0, 0)$ for every $c > c^\star$, whenever the initial data (N_0, u_0) is compactly supported. Considering compactly supported initial data is crucial from the point of view of biological applications.

2. Presentation of the model

Let us denote by $n(t, x, a)$ (respectively, $p(t, x, a)$), the quiescent (respectively, proliferating) HSC population density, at time t and position $x \in \Omega$, which have spent a time a in their compartment. We consider here an unbounded one-dimensional domain, $\Omega = (-\infty, +\infty)$. Quiescent cells can either be lost at a rate $\delta \geq 0$, which takes into account the cellular differentiation, or can be introduced in the proliferating phase with a rate $\beta \geq 0$. Proliferating cells can be eliminated by apoptosis (programmed cell death) with a rate $\gamma \geq 0$. We denote by $r \geq 0$ the duration of the proliferating phase. At the end of the proliferating phase of the cell cycle, each cell divides by mitosis into two daughter cells. A part ($K \in [0, 1]$) of daughter cells returns immediately to the proliferating phase to divide again while the other part ($(1 - K) \in [0, 1]$) enters directly the quiescent phase. In this work, we suppose that the rates δ and β depend upon the total population of quiescent cells at time t and location x

$$N(t, x) = \int_0^{+\infty} n(t, x, a)\mathrm{d}a.$$

We denote by $d_1 > 0$ (respectively, $d_2 > 0$) the diffusion rate of quiescent (respectively, proliferating) cells. Throughout this paper, we make the following hypotheses on the functions β and δ.

The function $N \mapsto \beta(N)$ is continuously differentiable on $\mathbb{R}$ and decreasing on $\mathbb{R}^+$ with $\lim_{N\to+\infty} \beta(N) = 0$. (1)

The function $N \mapsto \delta(N)$ is continuously differentiable on $\mathbb{R}$ and increasing on $\mathbb{R}^+$. (2)

Typically, β is modeled by a Hill function, [24, 29, 30], given on $\mathbb{R}^+$ by

$$\beta(N) = \frac{\beta_0 \theta^\alpha}{\theta^\alpha + N^\alpha}, \qquad \alpha > 1, \tag{3}$$

where β_0 is the maximal rate of the transition between quiescent phase and proliferating one, θ is the value for which β attains half of its maximum value, and α is the sensitivity of the rate of reintroduction. It describes the change of reintroduction rate due to external stimuli, such as growth factors.

An example of δ is given on $\mathbb{R}^+$ by the following expression

$$\delta(N) = \hat{\delta} N^\kappa, \quad \hat{\delta} > 0 \quad \text{and} \quad \kappa \geq 1.$$

The evolution of the HSC population is described, for $t > 0$ and $x \in \mathbb{R}$, by the following system of age and space structured partial differential system

$$\left\{ \begin{array}{rcll} \dfrac{\partial n}{\partial t} + \dfrac{\partial n}{\partial a} & = & d_1 \dfrac{\partial^2 n}{\partial x^2} - (\delta(N(t,x)) + \beta(N(t,x)))n, & a > 0, \\ \dfrac{\partial p}{\partial t} + \dfrac{\partial p}{\partial a} & = & d_2 \dfrac{\partial^2 p}{\partial x^2} - \gamma p, & 0 < a < r. \end{array} \right. \tag{4}$$

This system is completed, for $t > 0$ and $x \in \mathbb{R}$, by the following boundary conditions

$$\left\{ \begin{array}{rcl} n(t,x,0) & = & 2(1-K)p(t,x,r), \\ p(t,x,0) & = & \beta(N(t,x))N(t,x) + 2Kp(t,x,r), \\ n(t,x,+\infty) & = & 0, \end{array} \right. \tag{5}$$

and the initial conditions, for $x \in \mathbb{R}$,

$$\left\{ \begin{array}{rcll} n(0,x,a) & = & n_0(x,a), & a > 0, \\ p(0,x,a) & = & p_0(x,a), & 0 < a < r. \end{array} \right.$$

The first equation of (5) describes the portion of new quiescent cells coming from the proliferating phase with a rate $1-K$ (the coefficient 2 represents the division of cells at the end of the proliferating phase). The second equation represents the flux of cells from quiescent phase to the proliferating one with a rate β over all age $a \in (0, +\infty)$, and the portion K of dividing cells that return to the proliferating phase to divide again. Natural boundary conditions in space are given by

$$|n(t, \pm\infty, a)| < +\infty,\ t \geq 0,\ a \geq 0 \text{ and } |p(t, \pm\infty, a)| < +\infty,\ t \geq 0,\ 0 \leq a \leq r.$$

3. Reduction to a coupled reaction-diffusion and difference equations with delay

Let $X = BUC(\mathbb{R}, \mathbb{R})$ be the Banach space of all bounded and uniformly continuous functions from $\mathbb{R}$ to $\mathbb{R}$ with the usual supremum norm $|\cdot|_X$ and $X^+ := \{\phi \in X : \phi(x) \geq 0,\ \text{for all } x \in \mathbb{R}\}$. The space X is a Banach lattice under the partial ordering induced by the closed cone X^+. Consider the one-dimensional heat equation

$$\begin{cases} \dfrac{\partial w(t,x)}{\partial t} &= d_i \dfrac{\partial^2 w(t,x)}{\partial x^2}, \quad t > 0,\ x \in \mathbb{R}, \\ w(0,x) &= w_0(x), \qquad\qquad x \in \mathbb{R}, \end{cases} \tag{6}$$

with $i = 1, 2$ and $w_0 \in X$. The solution $w(t,x)$ of (6) can be expressed in terms of the Green's function

$$\Gamma_i(t,x) = \frac{1}{2\sqrt{d_i \pi t}} \exp\left(-\frac{x^2}{4 d_i t}\right), \quad t > 0,\ x \in \mathbb{R}.$$

More precisely,

$$w(t,x) = \int_{-\infty}^{+\infty} \Gamma_i(t, x-y) w_0(y) \mathrm{d}y, \quad t > 0,\ x \in \mathbb{R},$$

with

$$\int_{-\infty}^{+\infty} \Gamma_i(t,x) \mathrm{d}x = 1, \quad \text{for all} \quad t > 0. \tag{7}$$

It is important to remark that the solutions of (6) are well defined for initial conditions given on the space X. More precisely, if we put

$$(T_i(t) w_0)(x) := \int_{-\infty}^{+\infty} \Gamma_i(t, x-y) w_0(y) \mathrm{d}y, \quad t > 0,\ x \in \mathbb{R},$$

we obtain (see for instance [42]) an analytic semigroup $T_i(t) : X \to X$ such that $T_i(t)X^+ \subset X^+$, for all $t \geq 0$.

By integrating the first equation of (4) over the age and using the boundary conditions (5), we obtain

$$\frac{\partial N(t,x)}{\partial t} = d_1 \frac{\partial^2 N(t,x)}{\partial x^2} - (\delta(N(t,x)) + \beta(N(t,x)))N(t,x) + 2(1-K)p(t,x,r).$$

We integrate the second equation of (4) along characteristics by setting $w_s(t,x) = p(t,x,t+s)$, $s \in \mathbb{R}$. Then, for $t > t_0 := \max\{0, -s\}$ and $x \in \mathbb{R}$, the equation of p becomes

$$\begin{cases} \dfrac{\partial w_s(t,x)}{\partial t} &= d_2 \dfrac{\partial^2 w_s(t,x)}{\partial x^2} - \gamma w_s(t,x), \\ w_s(t_0,x) &= p(t_0,x,t_0+s). \end{cases}$$

Using the Green's function, we get

$$w_s(t,x) = e^{-\gamma(t-t_0)} \int_{-\infty}^{+\infty} \Gamma_2(t-t_0, x-y) w_s(t_0,y) \mathrm{d}y, \quad t > t_0 \quad x \in \mathbb{R}.$$

This yields the following expression

$$p(t,x,r) = \begin{cases} e^{-\gamma t} \displaystyle\int_{-\infty}^{+\infty} \Gamma_2(t, x-y) p_0(y, r-t) \mathrm{d}y, & t \leq r, \\ e^{-\gamma r} \displaystyle\int_{-\infty}^{+\infty} \Gamma_2(r, x-y) p(t-r, y, 0) \mathrm{d}y, & t > r. \end{cases}$$

Because we are interested in the asymptotic behavior of solutions, we suppose that $t > r$ and we assume that the whole past is given in the domain $[0,r] \times \mathbb{R}$. From now on, we make a translation of the initial conditions so as to define them on the domain $[-r,0] \times \mathbb{R}$. We put $u(t,x) = p(t,x,0)$, for $t > 0$ and $x \in \mathbb{R}$. Then, we focus on the study of the system, for $t > 0$ and $x \in \mathbb{R}$,

$$\begin{cases} \dfrac{\partial N(t,x)}{\partial t} = d_1 \dfrac{\partial^2 N(t,x)}{\partial x^2} - (\delta(N(t,x)) + \beta(N(t,x)))N(t,x) \\ \qquad\qquad + 2(1-K)e^{-\gamma r} \displaystyle\int_{-\infty}^{+\infty} \Gamma_2(r, x-y) u(t-r, y) \mathrm{d}y, \\ u(t,x) = \beta(N(t,x))N(t,x) + 2Ke^{-\gamma r} \displaystyle\int_{-\infty}^{+\infty} \Gamma_2(r, x-y) u(t-r, y) \mathrm{d}y, \end{cases} \tag{8}$$

with initial conditions

$$N(0,x) = N_0(x) \quad \text{and} \quad u(\theta,x) = u_0(\theta,x), \quad \text{for } \theta \in [-r,0],\ x \in \mathbb{R}.$$

Comparison of (4)-(5) with (8) shows the non-local effect that is caused by cells moving during proliferating phase.

4. Existence, uniqueness and positivity of solutions

First, we observe that by the method of steps we can solve the system (8) in each interval $[kr,(k+1)r]$, for $k = 0,1,\dots$. However, by this method the problem of regularity of the solutions is not well considered. To deal with this problem, we use the technique of constructing two monotones sequences of bounded lower and upper solutions, which converge to the unique solution of (8). We will start by establishing the uniqueness and positivity of bounded solutions $(N(t,x),u(t,x))$ of (8).

Consider the Banach space $C := C\left([-r,0],X\right)$ of continuous functions from $[-r,0]$ into X with the classical supremum norm $\|\cdot\|_C$ and the closed cone $C^+ := C\left([-r,0],X^+\right)$. We identify the functions $N,u : [0,b)\times\mathbb{R} \to \mathbb{R}$, $b>0$, (respectively, $u_0 : [-r,0]\times\mathbb{R}\to\mathbb{R}$) as functions from $[0,b)$ (respectively, $[-r,0]$) into X, by putting $N(t)(x) = N(t,x)$ and $u(t)(x) = u(t,x)$ (respectively, $u_0(\theta)(x) = u_0(\theta,x)$).

Consider the nonlinear functions f, $g : X \to X$ defined, for $v \in X$, by

$$f(v)(x) = \left(\delta(v(x)) + \beta(v(x))\right)v(x) \quad \text{and} \quad g(v)(x) = \beta(v(x))v(x), \quad x \in \mathbb{R}.$$

Due to (1) and (2), the functions f and g are continuously differentiable on X and satisfy $f(X^+) \subseteq X^+$, $g(X^+) \subseteq X^+$. The system (8) reads, for $t>0$,

$$\left\{\begin{array}{lcl} \dfrac{\mathrm{d}N(t)}{\mathrm{d}t} &=& d_1\Delta N(t) - f(N(t)) + 2(1-K)e^{-\gamma r}T_2(r)u(t-r), \\ u(t) &=& g(N(t)) + 2Ke^{-\gamma r}T_2(r)u(t-r), \end{array}\right. \tag{9}$$

with initial conditions

$$N(0) = N_0 \in X^+ \quad \text{and} \quad u(\theta) = u_0(\theta), \quad \theta \in [-r,0],\ u_0 \in C^+.$$

An abstract integral formulation of the system (8) (or equivalently (9)) (in terms of the semigroup $T_1(t)$) is

$$\left\{\begin{array}{lcl} N(t) &=& T_1(t)N_0 - \displaystyle\int_0^t T_1(t-s)f(N(s))\mathrm{d}s \\ && \qquad\qquad +2(1-K)e^{-\gamma r}\displaystyle\int_0^t T_1(t-s)T_2(r)u(s-r)\mathrm{d}s, \\ u(t) &=& g(N(t)) + 2Ke^{-\gamma r}T_2(r)u(t-r). \end{array}\right. \tag{10}$$

The solutions of (10) are called mild solutions of (8) (or (9)). Since the semigroup $T_1(t)$ is analytic, such mild solutions are also classical solutions of (8) (or (9)) (see [42], Corollary 2.5, page 50). The systems (8) (or (9)) and (10) are equivalent.

The next result proves the uniqueness of bounded solutions.

Proposition 1. *Suppose that the hypothesis* (1) *and* (2) *are fulfilled. Then, for each initial condition* $(N_0, u_0) \in X \times C$*, the system* (10) *has at most one bounded solution.*

Proof. Since the functions β and δ are continuously differentiable, then the functions f and g are also continuously differentiable. Let consider (N^1, u^1) and (N^2, u^2) two bounded solutions of (10) defined on an interval $[0, b)$, $b > 0$, with the same initial condition $(N_0, u_0) \in X \times C$. We put $N = N^1 - N^2$ and $u = u^1 - u^2$. Then, (10) gives

$$\left\{ \begin{array}{rcl} N(t) & = & -\displaystyle\int_0^t T_1(t-s)\left(f(N^1(s)) - f(N^2(s))\right)\mathrm{d}s \\ & & \qquad\qquad +2(1-K)e^{-\gamma r}\displaystyle\int_0^t T_1(t-s)T_2(r)u(s-r)\mathrm{d}s, \\ u(t) & = & g(N^1(t)) - g(N^2(t)) + 2Ke^{-\gamma r}T_2(r)u(t-r). \end{array} \right.$$

Define $n = \lfloor b/r \rfloor$. We decompose the interval $[0, b)$ into $[0, r] \cup [r, 2r] \cup \ldots \cup [nr, b)$, and we proceed by steps in each subinterval. Let $t \in [0, r]$. For all $s \in [0, t]$, $u(s - r) = 0$. Then,

$$\left\{ \begin{array}{rcl} N(t) & = & -\displaystyle\int_0^t T_1(t-s)\left(f(N^1(s)) - f(N^2(s))\right)\mathrm{d}s, \\ u(t) & = & g(N^1(t)) - g(N^2(t)). \end{array} \right.$$

As N^1 and N^2 are bounded, there exists $R > 0$ such that $|N^1(s)|_X, |N^2(s)|_X < R$, for all $s \in [0, r]$. Because of the continuity property of β' and δ', there exists $L_R > 0$ such that

$$\left\{ \begin{array}{rcccl} |f(N^1(s)) - f(N^2(s))|_X & \leq & L_R|N^1(s) - N^2(s)|_X & = & L_R|N(s)|_X, \\ |g(N^1(s)) - g(N^2(s))|_X & \leq & L_R|N^1(s) - N^2(s)|_X & = & L_R|N(s)|_X. \end{array} \right.$$

Furthermore, $|T_1(t)\phi|_X \leq |\phi|_X$ for all $t \geq 0$ and $\phi \in X$. Then, we obtain

$$|N(t)|_X \leq L_R \int_0^t |N(s)|_X \mathrm{d}s \quad \text{and} \quad |u(t)|_X \leq L_R|N(t)|_X, \quad t \in [0, r].$$

By Gronwall's lemma, we conclude that $N(t)(x) = u(t)(x) = 0$, for all $t \in [0, r]$ and $x \in \mathbb{R}$. Applying the same arguments in each interval $[kr, (k+1)r]$, we conclude that $N(t) = u(t) = 0$, for all $t \in [0, b)$. This completes the proof. $\square$

The following proposition proves the positivity of bounded solutions of the system (8) (or (9)).

Proposition 2. *Assume that* (1) *and* (2) *hold. Let* $(N_0, u_0) \in X^+ \times C^+$ *and* (N, u) *be a bounded solution of* (8) *corresponding to* (N_0, u_0)*. Then,* (N, u) *is nonnegative.*

Proof. Let $[0, b)$ be the interval of existence of (N, u). We put $U(t) = e^{-\rho t} N(t)$, for $\rho > 0$. Then, the first equation of (8) implies

$$\frac{\mathrm{d}U(t)}{\mathrm{d}t} = d_1 \Delta U(t) - l_\rho(t) U(t) + 2(1-K) e^{-\gamma r} e^{-\rho t} T_2(r) u(t-r),$$

with $l_\rho(t) = \rho + [\delta(N(t)) + \beta(N(t))]$, for $t \in [0, b)$. Due to the fact that N is bounded, we can take $\rho > 0$ large enough to ensure that $l_\rho(t) \geq 0$, for all $t \in [0, b)$. We use an iterative method on $[0, b) = [0, r] \cup [r, 2r] \cup \ldots \cup [nr, b)$, with $n = \lfloor b/r \rfloor$. Let $t \in [0, r]$. As $t - r \in [-r, 0]$, the above inequality becomes

$$\begin{cases} \dfrac{\mathrm{d}U(t)}{\mathrm{d}t} - d_1 \Delta U(t) + l_\rho(t) U(t) = 2(1-K) e^{-\gamma r} e^{-\rho t} T_2(r) u_0(t-r) \geq 0, \\ U(0) = N_0 \geq 0. \end{cases}$$

As $l_\rho(t) \geq 0$, by the maximum principle (see [28], Theorem 10, Chapter 3, Section 6) we get $U(t) \geq 0$ for $t \in [0, r]$. That is to say that $N(t, x) \geq 0$, for all $(t, x) \in [0, r] \times \mathbb{R}$. Moreover, the second equation of (8) implies that $u(t, x) \geq 0$, for all $(t, x) \in [0, r] \times \mathbb{R}$. We repeat the same argument for $t \in [kr, (k+1)r]$, with $k = 1, 2, \ldots, n$. Then, we obtain

$$N(t, x) \geq 0 \quad \text{and} \quad u(t, x) \geq 0, \quad \text{for all} \quad (t, x) \in [0, b) \times \mathbb{R}.$$

$\square$

Now, we return to the existence of solutions of (8). We need to define the notion of upper and lower solutions of (8).

Definition 1. *A pair of functions* $(\overline{N}, \overline{u})$ *(respectively,* $(\underline{N}, \underline{u})$*), is called upper (respectively, lower) solution of* (8) *on* $[0, b)$*,* $b > 0$*, if* $\overline{N}$ *(respectively,*

$\underline{N}$) is C^1 in $t \in (0, b)$, C^2 in $x \in \mathbb{R}$, $\overline{u}$ (respectively, $\underline{u}$) is in $C([-r, b), X)$, and they satisfy the following inequalities

$$\begin{cases} \dfrac{\mathrm{d}\overline{N}(t)}{\mathrm{d}t} & \geq \quad d_1 \Delta \overline{N}(t) - f(\overline{N}(t)) + 2(1-K)e^{-\gamma r} T_2(r) \overline{u}(t-r), \\ \overline{u}(t) & \geq \quad \beta(\underline{N}(t))\overline{N}(t) + 2K e^{-\gamma r} T_2(r) \overline{u}(t-r), \end{cases} \tag{11}$$

and

$$\begin{cases} \dfrac{\mathrm{d}\underline{N}(t)}{\mathrm{d}t} & \leq \quad d_1 \Delta \underline{N}(t) - f(\underline{N}(t)) + 2(1-K)e^{-\gamma r} T_2(r) \underline{u}(t-r), \\ \underline{u}(t) & \leq \quad \beta(\overline{N}(t))\underline{N}(t) + 2K e^{-\gamma r} T_2(r) \underline{u}(t-r). \end{cases}$$

A nonnegative bounded upper (respectively, lower) solution $(\overline{N}, \overline{u})$ (respectively, $(\underline{N}, \underline{u})$) of (8) satisfies the following proposition.

Proposition 3. *Suppose that* (1)-(2) *hold. Let* $(\overline{N}, \overline{u})$ *(respectively,* $(\underline{N}, \underline{u})$*) be a nonnegative and bounded upper (respectively, lower) solution of* (8) *on* $[0, b)$*,* $b > 0$*, such that* $\underline{N}(0) \leq \overline{N}(0)$ *and* $\underline{u}(\theta) \leq \overline{u}(\theta)$*, for* $-r \leq \theta \leq 0$*. Then,* $\underline{N}(t) \leq \overline{N}(t)$ *and* $\underline{u}(t) \leq \overline{u}(t)$*, for all* $t \in [0, b)$*.*

Proof. We put

$$N = \overline{N} - \underline{N}, \quad \text{on} \quad [0, b) \times \mathbb{R} \quad \text{and} \quad u = \overline{u} - \underline{u}, \quad \text{on} \quad [-r, b) \times \mathbb{R}.$$

We obtain the following inequalities

$$\begin{cases} \dfrac{\mathrm{d}N(t)}{\mathrm{d}t} - d_1 \Delta N(t) + f(\overline{N}(t)) - f(\underline{N}(t)) \geq 2(1-K)e^{-\gamma r} T_2(r) u(t-r), \\ u(t) \geq \beta(\underline{N}(t))\overline{N}(t) - \beta(\overline{N}(t))\underline{N}(t) + 2K e^{-\gamma r} T_2(r) u(t-r), \end{cases}$$

with $N(0) = \overline{N}(0) - \underline{N}(0) \geq 0$ and $u(t) = \overline{u}(t) - \underline{u}(t) \geq 0$, for $t \in [-r, 0]$. We use the same iterative idea as in the proof of Proposition 2. By steps, let $t \in [0, r]$. Then, $t - r \in [-r, 0]$ and $u(t-r) = \overline{u}(t-r) - \underline{u}(t-r) \geq 0$. In addition, as the functions β and δ are continuously differentiable and by using the mean value theorem, we obtain

$$f(\overline{N}(t)) - f(\underline{N}(t)) = f'\left((1 - c(t))\overline{N}(t) + c(t)\underline{N}(t)\right) N(t), \quad t \in [0, r],$$

for some $c(t) \in [0, 1]$, with $f'(v)(x) = (\beta'(v(x)) + \delta'(v(x)))\, v(x) + \beta(v(x)) + \delta(v(x))$, for $v \in X^+$ and $x \in \mathbb{R}$. Consequently,

$$\begin{cases} \dfrac{\mathrm{d}N(t)}{\mathrm{d}t} - d_1 \Delta N(t) + f'(\nu(t))\, N(t) \geq 0, \quad t \in [0, r], \\ N(0) \geq 0, \end{cases} \tag{12}$$

with $\nu(t) = (1 - c(t))\overline{N}(t) + c(t)\underline{N}(t)$, $t \in [0, r]$. Hence, as in the proof of Proposition 2, we put $U(t) = e^{-\rho t} N(t)$. Then for $\rho > 0$ large enough, we obtain that $U(t) \geq 0$ for $t \in [0, r]$. This leads to

$$N(t) = \overline{N}(t) - \underline{N}(t) \geq 0, \quad \text{for } t \in [0, r].$$

Furthermore, as $\overline{N}(t) \geq \underline{N}(t)$ for $t \in [0, r]$ and β increasing, we obtain

$$\beta(\underline{N}(t))\overline{N}(t) - \beta(\overline{N}(t))\underline{N}(t) = \beta(\overline{N}(t))N(t) + \left[\beta(\underline{N}(t)) - \beta(\overline{N}(t))\right]\overline{N}(t) \geq 0.$$

Then, (1) implies

$$\beta(\underline{N}(t))\overline{N}(t) - \beta(\overline{N}(t))\underline{N}(t) \geq \beta(\overline{N}(t))N(t).$$

Consequently, we obtain

$$u(t) \geq \beta(\overline{N}(t))N(t) + 2Ke^{-\gamma r}T_2(r)u(t - r) \geq 0, \quad t \in [0, r].$$

This means that

$$\underline{u}(t) \leq \overline{u}(t), \quad \text{for } t \in [0, r].$$

We repeat the same argument on the intervals $[r, 2r]$, $[2r, 3r], \ldots,$ and we obtain

$$\underline{N}(t) \leq \overline{N}(t) \quad \text{and} \quad \underline{u}(t) \leq \overline{u}(t), \quad \text{for } t \in [0, b).$$

The proof is complete. $\square$

The following theorem gives the existence of solutions of (8). The positivity and uniqueness follow from the previous results.

Theorem 1. *Suppose that* (1)-(2) *hold and let* $(N_0, u_0) \in X^+ \times C^+$. *If* (8) *has nonnegative bounded upper and lower solutions* $(\overline{N}, \overline{u})$, $(\underline{N}, \underline{u})$ *on* $[0, b)$, $b > 0$, *such that* $0 \leq \underline{N}(0) \leq N_0 \leq \overline{N}(0)$ *and* $0 \leq \underline{u}(\theta) \leq u_0(\theta) \leq \overline{u}(\theta)$, *for* $-r \leq \theta \leq 0$, *then it has a solution* (N, u) *defined on* $[0, b)$. *Furthermore,* (N, u) *satisfies*

$$0 \leq \underline{N}(t) \leq N(t) \leq \overline{N}(t) \quad \text{and} \quad 0 \leq \underline{u}(t) \leq u(t) \leq \overline{u}(t), \ \text{for } t \in [0, b).$$

Proof. The upper and lower solutions are bounded. Then, there exists $R > 0$ such that $0 \leq \underline{N}(t) \leq \overline{N}(t) \leq R$, for all $t \in [0, b)$. As β' and δ' are continuous, there exists $L_R > 0$ such that $-L_R \leq f'(\zeta)(x) \leq L_R$, for $x \in \mathbb{R}$, $\zeta \in X^+$

and $|\zeta|_X \le R$. We define two sequences $\{(\overline{N}^k, \overline{u}^k)\}_{k=1}^{+\infty}$ and $\{(\underline{N}^k, \underline{u}^k)\}_{k=1}^{+\infty}$ solutions on $[0, b)$ of the following systems

$$\begin{cases} \dfrac{\mathrm{d}\overline{N}^k(t)}{\mathrm{d}t} = d_1\Delta\overline{N}^k(t) - (\delta(\overline{N}^{k-1}(t)) + \beta(\overline{N}^{k-1}(t)))\overline{N}^k(t) \\ \qquad\qquad +L_R(\overline{N}^{k-1}(t) - \overline{N}^k(t)) + 2(1-K)e^{-\gamma r}T_2(r)\overline{u}^{k-1}(t-r), \\ \overline{u}^k(t) = \beta(\underline{N}^{k-1}(t))\overline{N}^k(t) + 2Ke^{-\gamma r}T_2(r)\overline{u}^{k-1}(t-r), \end{cases} \tag{13}$$

and

$$\begin{cases} \dfrac{\mathrm{d}\underline{N}^k(t)}{\mathrm{d}t} = d_1\Delta\underline{N}^k(t) - (\delta(\underline{N}^{k-1}(t)) + \beta(\underline{N}^{k-1}(t)))\underline{N}^k(t) \\ \qquad\qquad +L_R(\underline{N}^{k-1}(t) - \underline{N}^k(t)) + 2(1-K)e^{-\gamma r}T_2(r)\underline{u}^{k-1}(t-r), \\ \underline{u}^k(t) = \beta(\overline{N}^{k-1}(t))\underline{N}^k(t) + 2Ke^{-\gamma r}T_2(r)\underline{u}^{k-1}(t-r), \end{cases} \tag{14}$$

with $\overline{N}^k(0) = \underline{N}^k(0) = N_0$, $\overline{u}^k(\theta) = \underline{u}^k(\theta) = u_0(\theta)$, $-r \le \theta \le 0$, for $k = 1, 2, \ldots$, and for $k = 0$, we put $(\underline{N}^0, \underline{u}^0) = (\underline{N}, \underline{u})$ and $(\overline{N}^0, \overline{u}^0) = (\overline{N}, \overline{u})$.

It is clear that the two sequences $\{(\overline{N}^k, \overline{u}^k)\}_{k=0}^{+\infty}$, $\{(\underline{N}^k, \underline{u}^k)\}_{k=0}^{+\infty}$ are well defined. First, we will prove by induction that $(\overline{N}^k, \overline{u}^k)$, $(\underline{N}^k, \underline{u}^k)$ are upper and lower solutions of (8) and

$$\begin{cases} \underline{N}^0 \le \underline{N}^1 \le \ldots \le \underline{N}^k \le \overline{N}^k \le \ldots \le \overline{N}^1 \le \overline{N}^0, \\ \underline{u}^0 \le \underline{u}^1 \le \ldots \le \underline{u}^k \le \overline{u}^k \le \ldots \le \overline{u}^1 \le \overline{u}^0. \end{cases}$$

For $k = 0$, we have $(\overline{N}^0, \overline{u}^0) = (\overline{N}, \overline{u})$ and $(\underline{N}^0, \underline{u}^0) = (\underline{N}, \underline{u})$. Then, $(\overline{N}^0, \overline{u}^0)$, $(\underline{N}^0, \underline{u}^0)$ are upper and lower solutions. Furthermore, by Proposition 3, $\underline{N}^0 \le \overline{N}^0$ and $\underline{u}^0 \le \overline{u}^0$. On the other hand, by (13) and (11) we have

$$\begin{cases} \dfrac{\mathrm{d}\overline{N}^1(t)}{\mathrm{d}t} = d_1\Delta\overline{N}^1(t) - (\delta(\overline{N}^0(t)) + \beta(\overline{N}^0(t)))\overline{N}^1(t) + L_R(\overline{N}^0(t) - \overline{N}^1(t)) \\ \qquad\qquad\qquad\qquad +2(1-K)e^{-\gamma r}T_2(r)\overline{u}^0(t-r), \\ \overline{u}^1(t) = \beta(\underline{N}^0(t))\overline{N}^1(t) + 2Ke^{-\gamma r}T_2(r)\overline{u}^0(t-r), \end{cases} \tag{15}$$

and

$$\begin{cases} \dfrac{\mathrm{d}\overline{N}^0(t)}{\mathrm{d}t} \ge d_1\Delta\overline{N}^0(t) - f(\overline{N}^0(t)) + 2(1-K)e^{-\gamma r}T_2(r)\overline{u}^0(t-r), \\ \overline{u}^0(t) \ge \beta(\underline{N}^0(t))\overline{N}^0(t) + 2Ke^{-\gamma r}T_2(r)\overline{u}^0(t-r). \end{cases}$$

Then, if we put $\hat{N}^0 = \overline{N}^1 - \overline{N}^0$ and $\hat{u}^0 = \overline{u}^1 - \overline{u}^0$, we obtain

$$\begin{cases} \frac{\mathrm{d}\hat{N}^0(t)}{\mathrm{d}t} & \leq & d_1\Delta\hat{N}^0(t) - (\delta(\overline{N}^0(t)) + \beta(\overline{N}^0(t)))\hat{N}^0(t) - L_R\hat{N}^0(t), \\ \hat{u}^0(t) & \leq & \beta(\underline{N}^0(t))\hat{N}^0(t), \end{cases}$$

with $\hat{N}^0(0) \leq 0$ and $\hat{u}^0(\theta) \leq 0$, for $-r \leq \theta \leq 0$. Consequently, by the principle of maximum, we obtain $\hat{N}^0 \leq 0$ and $\hat{u}^0 \leq 0$. Thus, $\overline{N}^0 \geq \overline{N}^1$ and $\overline{u}^0 \geq \overline{u}^1$. Likewise, using the same technique we prove that $\underline{N}^0 \leq \underline{N}^1$ and $\underline{u}^0 \leq \underline{u}^1$. Thanks to (15) and the fact that $\overline{N}^0 \geq \overline{N}^1$ and $\overline{u}^0 \geq \overline{u}^1$, we have

$$\begin{cases} \dfrac{\mathrm{d}\overline{N}^1(t)}{\mathrm{d}t} \geq d_1\Delta\overline{N}^1(t) - f(\overline{N}^1(t)) - \Big(f(\overline{N}^0(t)) - f(\overline{N}^1(t))\Big) \\ \qquad\qquad\qquad + L_R(\overline{N}^0(t) - \overline{N}^1(t)) + 2(1-K)e^{-\gamma r}T_2(r)\overline{u}^1(t-r), \\ \overline{u}^1(t) \geq \beta(\underline{N}^0(t))\overline{N}^1(t) + 2Ke^{-\gamma r}T_2(r)\overline{u}^1(t-r), \end{cases}$$

with

$$f(\overline{N}^0(t)) - f(\overline{N}^1(t)) \leq L_R(\overline{N}^0(t) - \overline{N}^1(t)) \quad \text{and} \quad \beta(\underline{N}^0(t)) \geq \beta(\underline{N}^1(t)).$$

Then,

$$\begin{cases} \dfrac{\mathrm{d}\overline{N}^1(t)}{\mathrm{d}t} \geq d_1\Delta\overline{N}^1(t) - f(\overline{N}^1(t)) + 2(1-K)e^{-\gamma r}T_2(r)\overline{u}^1(t-r), \\ \overline{u}^1(t) \geq \beta(\underline{N}^1(t))\overline{N}^1(t) + 2Ke^{-\gamma r}T_2(r)\overline{u}^1(t-r). \end{cases}$$

Using the same technique as above, we obtain

$$\begin{cases} \dfrac{\mathrm{d}\underline{N}^1(t)}{\mathrm{d}t} \leq d_1\Delta\underline{N}^1(t) - f(\underline{N}^1(t)) + 2(1-K)e^{-\gamma r}T_2(r)\underline{u}^1(t-r), \\ \underline{u}^1(t) \leq \beta(\overline{N}^1(t))\underline{N}^1(t) + 2Ke^{-\gamma r}T_2(r)\underline{u}^1(t-r). \end{cases}$$

We have proved that $(\overline{N}^1, \overline{u}^1)$, $(\underline{N}^1, \underline{u}^1)$ are upper and lower solutions of (8), with $\overline{N}^0 \geq \overline{N}^1$, $\overline{u}^0 \geq \overline{u}^1$, $\underline{N}^0 \leq \underline{N}^1$ and $\underline{u}^0 \leq \underline{u}^1$. Furthermore, Proposition 3 implies that $\underline{N}^1 \leq \overline{N}^1$ and $\underline{u}^1 \leq \overline{u}^1$. In the same way, we obtain by induction that, for all $k \in \mathbb{N}^*$, $(\overline{N}^k, \overline{u}^k)$, $(\underline{N}^k, \underline{u}^k)$ are upper and lower solutions and satisfy $\overline{N}^{k-1} \geq \overline{N}^k$, $\overline{u}^{k-1} \geq \overline{u}^k$, $\underline{N}^{k-1} \leq \underline{N}^k$, $\underline{u}^{k-1} \leq \underline{u}^k$, $\underline{N}^k \leq \overline{N}^k$ and $\underline{u}^k \leq \overline{u}^k$ (the two last comparisons are obtained by applying Proposition 3). We conclude that

$$\begin{cases} \underline{N}^0 \leq \underline{N}^1 \leq \ldots \leq \underline{N}^k \leq \overline{N}^k \leq \ldots \leq \overline{N}^1 \leq \overline{N}^0, \\ \underline{u}^0 \leq \underline{u}^1 \leq \ldots \leq \underline{u}^k \leq \overline{u}^k \leq \ldots \leq \overline{u}^1 \leq \overline{u}^0. \end{cases}$$

Since the sequences $\{(\underline{N}^k,\underline{u}^k)\}_{k=0}^{+\infty}$ and $\{(\overline{N}^k,\overline{u}^k)\}_{k=0}^{+\infty}$ are monotone and bounded, their limits, as k tends to $+\infty$, exist. We put, for $t\in[0,b)$,

$$\lim_{k\to+\infty}(\underline{N}^k(t),\underline{u}^k(t))=(\underline{X}(t),\underline{v}(t)) \quad \text{and} \quad \lim_{k\to+\infty}(\overline{N}^k(t),\overline{u}^k(t))=(\overline{X}(t),\overline{v}(t)).$$

It is clear that $\underline{X}(t)\le\overline{X}(t)$ and $\underline{v}(t)\le\overline{v}(t)$, for all $t\in[0,b)$. On the other hand, by using the abstract integral formulations of systems (13)-(14) and the fact that they are equivalent to the classical formulations, if k tends to $+\infty$, we obtain

$$\begin{cases} \dfrac{\mathrm{d}\overline{X}(t)}{\mathrm{d}t}=d_1\Delta\overline{X}(t)-(\delta(\overline{X}(t))+\beta(\overline{X}(t)))\overline{X}(t)+2(1-K)e^{-\gamma r}T_2(r)\overline{v}(t-r),\\ \overline{v}(t)=\beta(\underline{X}(t))\overline{X}(t)+2Ke^{-\gamma r}T_2(r)\overline{v}(t-r), \end{cases}$$

and

$$\begin{cases} \dfrac{\mathrm{d}\underline{X}(t)}{\mathrm{d}t}=d_1\Delta\underline{X}(t)-(\delta(\underline{X}(t))+\beta(\underline{X}(t)))\underline{X}(t)+2(1-K)e^{-\gamma r}T_2(r)\underline{v}(t-r),\\ \underline{v}(t)=\beta(\overline{X}(t))\underline{X}(t)+2Ke^{-\gamma r}T_2(r)\underline{v}(t-r). \end{cases}$$

Consequently, $(\underline{X},\underline{v})$ (respectively, $(\overline{X},\overline{v})$) can also be seen as upper (respectively, lower) solution of (8). Then by Proposition 3, we have $\underline{X}\ge\overline{X}$ and $\underline{v}\ge\overline{v}$. Consequently, $\underline{X}=\overline{X}$ and $\underline{v}=\overline{v}$. We conclude that $(N,u)=(\underline{X},\underline{v})=(\overline{X},\overline{v})$ is a solution of (8). The proof is complete. $\square$

Remark 1. (i) *The solution obtained by Theorem 1 is a classical solution in the sense that it is once continuously differentiable with respect to t and twice continuously differentiable with respect to x. This can be seen using the abstract integral representation* (10) *of the solutions. Furthermore, under the compatibility condition for the difference equation, it is not difficult to verify the continuity of u.*

(ii) *By Theorem 1, to prove the existence of solutions of the system* (8)*, it suffice to prove the existence of a pair of upper and lower solutions.*

Now, we will construct appropriate upper and lower solutions of (8). We simply look for constant upper and lower solutions. It is clear that $(0,0)$ is always a lower solution of (8). A couple of positive constants (η,σ) is upper solution of (8) associated to the lower solution $(0,0)$ if and only if

$$\begin{cases} f(\eta)\ge 2(1-K)e^{-\gamma r}\sigma,\\ \left(1-2Ke^{-\gamma r}\right)\sigma\ge\beta(0)\eta. \end{cases} \tag{16}$$

We add the following necessary condition.

$$2Ke^{-\gamma r} < 1. \tag{17}$$

So, the system (16) is equivalent to

$$\begin{cases} \dfrac{\beta(0)}{1-2Ke^{-\gamma r}} \leq \dfrac{1}{2(1-K)e^{-\gamma r}}(\delta(\eta)+\beta(\eta)), \\ \dfrac{\beta(0)}{1-2Ke^{-\gamma r}}\eta \leq \sigma \leq \dfrac{1}{2(1-K)e^{-\gamma r}}(\delta(\eta)+\beta(\eta))\eta. \end{cases} \tag{18}$$

Corollary 1. *Suppose that* (1), (2) *and* (17) *are satisfied. Let* (η, σ) *be satisfying* (18) *and* $(N_0, u_0) \in X^+ \times C^+$ *be such that* $0 \leq N_0(x) \leq \eta$, *for* $x \in \mathbb{R}$ *and* $0 \leq u_0(\theta, x) \leq \sigma$, *for* $-r \leq \theta \leq 0$ *and* $x \in \mathbb{R}$. *Then, there exists a unique nonnegative bounded solution* (N, u) *of* (8). *Furthermore,* (N, u) *satisfies*

$$0 \leq N(t) \leq \eta, \quad 0 \leq u(t) \leq \sigma, \quad \text{for all} \quad t \geq 0.$$

Proof. This corollary is a direct consequence of Theorem 1. $\square$

Assume that δ satisfies

$$\lim_{N \mapsto +\infty} \delta(N) = +\infty. \tag{19}$$

Let $(N_0, u_0) \in X^+ \times C^+$. Then, $|N_0|_X < +\infty$ and $\|u_0\|_C < +\infty$. First, there exists $\eta > 0$ such that $|N_0|_X \leq \eta$ and

$$\frac{\beta(0)}{1-2Ke^{-\gamma r}} \leq \frac{1}{2(1-K)e^{-\gamma r}}(\delta(\eta)+\beta(\eta)).$$

Second, there exists $\sigma > 0$ such that $\|u_0\|_C \leq \sigma$ and

$$\frac{\beta(0)}{1-2Ke^{-\gamma r}}\eta \leq \sigma \leq \frac{1}{2(1-K)e^{-\gamma r}}(\delta(\eta)+\beta(\eta))\eta.$$

Then, we have proved the following corollary.

Corollary 2. *Suppose that* (1), (2), (17) *and* (19) *are satisfied. Let* $(N_0, u_0) \in X^+ \times C^+$. *Then, there exists a unique nonnegative bounded solution* (N, u) *of* (8).

5. Traveling wave fronts

A traveling wave solution of (8) is a special solution of the form

$$(N(t)(x), u(t)(x)) = (\phi(x+ct), \psi(x+ct)),$$

where $\phi, \psi \in C^2(\mathbb{R}, \mathbb{R}^+)$ and $c > 0$ is a constant corresponding to the wave speed (see [27, 37, 42]). Using the same notation, we consider the functions $f,\ g : \mathbb{R}^+ \to \mathbb{R}^+$, defined by

$$f(y) = (\delta(y) + \beta(y))\, y \quad \text{and} \quad g(y) = \beta(y) y, \quad y \in \mathbb{R}^+.$$

We put $z = x + ct$ and we substitute $(N(t)(x), u(t)(x))$ with $(\phi(z), \psi(z))$ into (8). We obtain the corresponding wave system

$$\begin{cases} c\phi'(z) = d_1\phi''(z) - f(\phi(z)) + 2(1-K)e^{-\gamma r} \left(T_2(r)\psi\right)(z - cr), \\ \psi(z) = g(\phi(z)) + 2Ke^{-\gamma r} \left(T_2(r)\psi\right)(z - cr). \end{cases} \tag{20}$$

If for some $c > 0$ the system (20) has a monotone solution (ϕ, ψ) defined on $\mathbb{R}$, subject to the following asymptotic condition

$$\phi(-\infty) = \psi(-\infty) = 0, \quad \phi(+\infty) = N^\star \quad \text{and} \quad \psi(+\infty) = u^\star, \tag{21}$$

where $(N^\star, u^\star)$ is a constant positive equilibrium of (8), then the corresponding solution $(N(t)(x), u(t)(x)) = (\phi(x+ct), \psi(x+ct))$ is called a traveling wave front with wave speed $c > 0$. We remark that $(N^\star, u^\star)$ is also a positive equilibrium of (20).

Let $A : X \to X$ be the bounded linear operator defined by

$$\left(A\psi\right)(z) = 2Ke^{-\gamma r} \left(T_2(r)\psi\right)(z - cr), \quad z \in \mathbb{R}.$$

Lemma 1. *Assume that* (17) *is satisfied. Then, the operator $Id - A$ is invertible and its inverse is given by*

$$(Id - A)^{-1}(\psi) = \xi * \psi, \quad \psi \in X,$$

where

$$\xi(z) = \sum_{n=0}^{+\infty} \xi_n(z), \quad z \in \mathbb{R}, \tag{22}$$

and

$$\xi_n(z) = \frac{(2Ke^{-\gamma r})^n}{2\sqrt{nd_2\pi r}} \exp\left(-\frac{(z - ncr)^2}{4nd_2 r}\right) = (2Ke^{-\gamma r})^n \Gamma_2(nr, z - ncr),\ z \in \mathbb{R},\ n \in \mathbb{N}.$$

Proof. Thanks to (7), we have $|T_2(r)|_{\mathcal{L}(X)} = 1$. Then, $|A|_{\mathcal{L}(X)} = 2Ke^{-\gamma r}$. So, the condition (17) is equivalent to

$$|A|_{\mathcal{L}(X)} < 1.$$

Furthermore,

$$\begin{aligned}
\left(A^n\psi\right)(z) &= \left(2Ke^{-\gamma r}\right)^n \left(T_2(nr)\psi\right)(z - ncr), \\
&= \frac{\left(2Ke^{-\gamma r}\right)^n}{2\sqrt{nd_2\pi r}} \int_{-\infty}^{+\infty} \exp\left(-\frac{(z-y-ncr)^2}{4nd_2 r}\right)\psi(y)\mathrm{d}y, \quad n \in \mathbb{N}^*.
\end{aligned}$$

Then, the operator $Id - A$ is invertible and its inverse is given by

$$\begin{aligned}
\left((Id - A)^{-1}\psi\right)(z) &= \sum_{n=0}^{+\infty} (A^n\psi)(z), \\
&= \int_{-\infty}^{+\infty} \sum_{n=0}^{+\infty} \frac{\left(2Ke^{-\gamma r}\right)^n}{2\sqrt{nd_2\pi r}} \exp\left(-\frac{(z-y-ncr)^2}{4nd_2 r}\right)\psi(y)\mathrm{d}y, \\
&= \int_{-\infty}^{+\infty} \xi(z-y)\psi(y)\mathrm{d}y, \\
&= \left(\xi * \psi\right)(z),
\end{aligned}$$

where ξ is given by (22). This completes the proof. $\square$

Remark 2. ξ_n, $n \in \mathbb{N}$, *has the following fundamental property*

$$\int_{-\infty}^{+\infty} \xi_n(y)\mathrm{d}y = \left(2Ke^{-\gamma r}\right)^n. \tag{23}$$

The system (20) becomes

$$\begin{cases} c\phi'(z) = d_1\phi''(z) - f(\phi(z)) + 2(1-K)e^{-\gamma r}\left(T_2(r)\psi\right)(z - cr), \\ \psi(z) = (\xi * g(\phi))(z), \end{cases} \tag{24}$$

with the notation $(\xi * g(\phi))(z) := \displaystyle\int_{-\infty}^{+\infty} \xi(z-y)g(\phi(y))\mathrm{d}y$, $z \in \mathbb{R}$. In fact, the system (24) can be reduced to the following single equation

$$c\phi'(z) = d_1\phi''(z) - f(\phi(z)) + 2(1-K)e^{-\gamma r}\left[T_2(r)\left(\xi * g(\phi)\right)\right](z - cr). \tag{25}$$

Remember that

$$T_2(r)\left(\xi * g(\phi)\right) = \Gamma_2(r,\cdot) * \left(\xi * g(\phi)\right) = \left(\Gamma_2(r,\cdot) * \xi\right) * g(\phi).$$

Let τ_a, $a \in \mathbb{R}$, be the translation operator defined on X^+ by $(\tau_a \psi)(z) = \psi(z-a)$. Then,

$$(T_2(r)\left(\xi * g(\phi)\right))(z-cr) = \left[\tau_{cr}\left(T_2(r)\left(\xi * g(\phi)\right)\right)\right](z) = \left[\left(\tau_{cr}\left(\Gamma_2(r,\cdot) * \xi\right)\right) * g(\phi)\right](z).$$

We put

$$\chi = \left(1 - 2Ke^{-\gamma r}\right) \tau_{cr}\left(\Gamma_2(r,\cdot) * \xi\right). \tag{26}$$

Then, $\chi : \mathbb{R} \to \mathbb{R}^+$ and

$$(T_2(r)\left(\xi * g(\phi)\right))(z-cr) = \frac{1}{1-2Ke^{-\gamma r}} \left(\chi * g(\phi)\right)(z).$$

(25) becomes

$$c\phi'(z) = d_1 \phi''(z) - f(\phi(z)) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left(\chi * g(\phi)\right)(z). \tag{27}$$

Lemma 2. *Assume that* (17) *is satisfied. Then, the function* χ *defined by* (26) *belongs to* $L^1(\mathbb{R}, \mathbb{R}^+)$ *and satisfies the following properties, for* $z \in \mathbb{R}$,

1. $\chi(z) = (1-2Ke^{-\gamma r}) \displaystyle\sum_{n=0}^{+\infty} (2Ke^{-\gamma r})^n \Gamma_2\left((n+1)r, z-(n+1)cr\right) > 0,$
2. $\displaystyle\int_{-\infty}^{+\infty} \chi(y)\mathrm{d}y = \left(1-2Ke^{-\gamma r}\right) \int_{-\infty}^{+\infty} \xi(y)\mathrm{d}y = 1,$
3. *there exists* $\lambda^-(c) < 0 < \lambda^+(c)$ *given by*

$$\lambda^{\pm}(c) := \frac{c}{2d_2}\left(1 \pm \sqrt{1 + \frac{4d_2}{rc^2}\ln\left(\frac{e^{\gamma r}}{2K}\right)}\right), \tag{28}$$

such that, for $\lambda \in (\lambda^-(c), \lambda^+(c))$,

$$1-2Ke^{-\gamma r}e^{d_2 r\lambda^2 - cr\lambda} > 0 \quad \text{and} \quad \left(\chi * e^{\lambda \cdot}\right)(z) = \frac{\left(1-2Ke^{-\gamma r}\right)e^{d_2 r \lambda^2 + (z-cr)\lambda}}{1-2Ke^{-\gamma r}e^{d_2 r\lambda^2 - cr\lambda}}. \tag{29}$$

Proof. (1) and (2) come from the definition of χ and the property (7).

Let $\lambda \in \mathbb{R}$. To prove (3), we first remark that the expression $\chi * e^{\lambda \cdot}$ is well defined. Second, by a sample calculation, we have the following fundamental property

$$\left(\Gamma_i(t,\cdot) * e^{\lambda \cdot}\right)(z) = e^{d_i t\lambda^2 + \lambda z}, \quad \text{for } t > 0, \ \ z \in \mathbb{R}.$$

Then,

$$\begin{aligned}\left(\chi * e^{\lambda\cdot}\right)(z) &= \left(1-2Ke^{-\gamma r}\right)e^{\lambda z}\sum_{n=0}^{+\infty}(2Ke^{-\gamma r})^n e^{d_2(n+1)r\lambda^2-(n+1)cr\lambda},\\ &= \left(1-2Ke^{-\gamma r}\right)e^{d_2 r\lambda^2+(z-cr)\lambda}\sum_{n=0}^{+\infty}\left(2Ke^{-\gamma r}e^{d_2 r\lambda^2-cr\lambda}\right)^n.\end{aligned}$$

We have to choose $\lambda \in \mathbb{R}$, such that

$$2Ke^{-\gamma r}e^{d_2 r\lambda^2-cr\lambda} < 1.$$

This is equivalent to

$$d_2 r\lambda^2 - cr\lambda - \ln\left(\frac{e^{\gamma r}}{2K}\right) < 0,$$

with $e^{\gamma r}/2K > 1$. The last inequality is satisfied for all $\lambda \in (\lambda^-(c), \lambda^+(c))$, with $\lambda^-(c)$ and $\lambda^+(c)$ given by (28). This completes the proof. $\square$

It is clear that if (ϕ, ψ) is a monotone solution of (20)-(21), then ϕ is a monotone solution of (27) and

$$\phi(-\infty) = 0 \quad \text{and} \quad \phi(+\infty) = N^\star. \tag{30}$$

To obtain the converse, we need the following assumption.

$$\text{The function } N \mapsto g(N) := \beta(N)N \text{ is increasing on } [0, N^\star]. \tag{31}$$

We have the following result.

Proposition 4. *Assume that* (17) *and* (31) *are satisfied. If* ϕ *is a monotone solution of* (27)-(30)*, then* $(\phi, \xi * g(\phi))$ *is a monotone solution of* (20)-(21)*, with*

$$u^\star = \frac{g(N^\star)}{1-2Ke^{-\gamma r}}.$$

Proof. Let ϕ be a solution of (27). Then, $(\phi, \xi * g(\phi))$ is a solution of (20). Suppose that ϕ is monotone and satisfies (30). Then, $0 \le \phi \le N^\star$ and thanks to (31), $\psi = \xi * g(\phi)$ is also monotone. Furthermore, the monotone convergence theorem implies that

$$\lim_{z\to-\infty}\psi(z) = \int_{-\infty}^{+\infty}\xi(y)\left(\lim_{z\to-\infty} g(\phi(z-y))\right)\mathrm{d}y = 0,$$

and

$$\lim_{z\to+\infty}\psi(z)=\int_{-\infty}^{+\infty}\xi(y)\left(\lim_{z\to+\infty}g(\phi(z-y))\right)\mathrm{d}y=\left(\int_{-\infty}^{+\infty}\xi(y)\mathrm{d}y\right)g(N^\star).$$

Then, from (22) and (23), we obtain

$$\lim_{z\to+\infty}\psi(z)=\frac{g(N^\star)}{1-2Ke^{-\gamma r}}.$$

This completes the proof. $\square$

Remark 3. *The hypothesis* (31) *is important to guarantee the existence of monotone traveling wave fronts. If we take the Hill function defined by* (3)*, we can see that* $N\mapsto g(N):=\beta(N)N$ *is an increasing function on* $\left[0,\theta/\sqrt[\alpha]{\alpha-1}\right]$. *Then to have* (31)*, we can choose* $N^\star\in\left(0,\theta/\sqrt[\alpha]{\alpha-1}\right]$.

We now look for the existence of steady states of (25) (or equivalently the steady states of (27)). Remark that the steady states of (25) are the uniform steady states of (8). Recall that 0 is always a steady state. A positive steady state $N^\star$ of (27) is given by

$$f(N^\star)=\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi*g(N^\star)\right)(z),\quad\text{for all } z\in\mathbb{R}.\tag{32}$$

As $N^\star$ is constant, we have

$$\left(\chi*g(N^\star)\right)(z)=\left(\int_{-\infty}^{+\infty}\chi(y)\mathrm{d}y\right)g(N^\star)=g(N^\star),\quad\text{for all } z\in\mathbb{R}.$$

Then, (32) becomes

$$f(N^\star)=\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}g(N^\star).$$

This is equivalent to

$$\delta(N^\star)=\frac{2e^{-\gamma r}-1}{1-2Ke^{-\gamma r}}\beta(N^\star).\tag{33}$$

We consider the function $h:[0,+\infty)\to[0,+\infty)$ defined by

$$h(N)=\frac{\delta(N)}{\beta(N)},\quad\text{for } N\in[0,+\infty).$$

Then, (33) is equivalent to

$$h(N^\star) = \frac{2e^{-\gamma r} - 1}{1 - 2Ke^{-\gamma r}}.$$

Thanks to (1) and (2), the function h is strictly increasing on $[0, +\infty)$ and satisfies $\lim_{N\to+\infty} h(N) = +\infty$. Then, the existence of positive steady state $N^\star$ is equivalent to

$$h(0) := \frac{\delta(0)}{\beta(0)} < \frac{2e^{-\gamma r} - 1}{1 - 2Ke^{-\gamma r}}.$$

In this case, $N^\star$ is given by

$$N^\star = h^{-1}\left(\frac{2e^{-\gamma r} - 1}{1 - 2Ke^{-\gamma r}}\right). \tag{34}$$

The existence of positive steady state $N^\star$ depends on the parameters r, K, γ and

$$\mu := \frac{1}{h(0)} = \frac{\beta(0)}{\delta(0)}.$$

For $\gamma > 0$, we define the following thresholds for the parameter r,

$$r_\mu = \begin{cases} \dfrac{1}{\gamma}\ln\left(\dfrac{2\mu}{\mu+1}\right), & \mu > 1, \\ 0, & 0 \le \mu \le 1, \end{cases}$$

whereas, for $\gamma = 0$,

$$r_\mu = \begin{cases} +\infty, & \mu > 1, \\ 0, & 0 \le \mu \le 1. \end{cases}$$

In particular, for $\mu = 0$, which corresponds to the case $\beta(0) = 0$ and $\delta(0) > 0$, we have $r_0 = 0$. The special case $\delta(0) = \beta(0) = 0$ can be treated directly, and will not be considered here. The notation

$$r_\infty = \frac{1}{\gamma}\ln(2),$$

corresponds to the case $\beta(0) > 0$, $\gamma > 0$ and $\delta(0) = 0$ ($\mu = \infty$). To introduce thresholds for the parameter K, we consider the function $K_\mu : [0, +\infty) \to [0, 1]$, defined by

$$K_\mu(r) = \begin{cases} 0, & r < r_\mu, \\ (1+\mu)\,K_0(r) - \mu, & r \ge r_\mu, \end{cases}$$

with the function $K_0 : [0, +\infty) \to [0, 1]$, given by

$$K_0(r) = \begin{cases} \dfrac{1}{2} e^{\gamma r}, & r < r_\infty, \\ 1, & r \geq r_\infty, \end{cases}$$

and in particular the function, for $\mu = \infty$,

$$\begin{array}{rcl} K_\infty : [0, +\infty) & \to & [0, 1], \\ r & \mapsto & K_\infty(r) = \begin{cases} 0, & r < r_\infty, \\ 1, & r \geq r_\infty. \end{cases} \end{array}$$

The functions $K_\mu(r)$ and $K_0(r)$ are represented in Figure 1, for $\mu > 1$ and $0 < \mu < 1$. In fact, it is easy to verify the validity of the following proposition

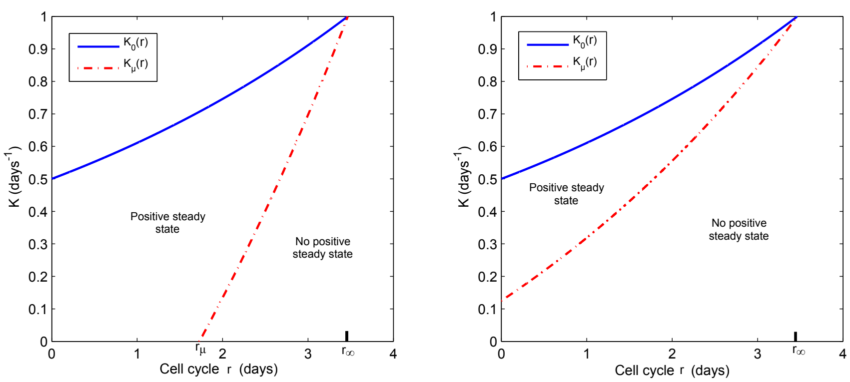

Figure 1: $K_0(r)$ and $K_\mu(r)$ are plotted to show in the $(r,\, K)$-plane the region of existence of uniforms steady states of system (8). Fixed parameter is $\gamma = 0.2$ day^{-1}. Left: $\mu = 2.40$. Right: $\mu = 0.75$. The zone of existence of uniform positive steady state is between the dashed curve $K_\mu(r)$ and the solid curve $K_0(r)$. Outside this area, the positive steady state does not exist. The intersection of $K_\mu(r)$ with the r-axis, for $\mu > 1$, is $\frac{1}{\gamma} \ln\left(\frac{2\mu}{\mu+1}\right)$, and with the K-axis, for $0 < \mu < 1$, is $\frac{1}{2}(1 - \mu)$.

concerning the existence and uniqueness of steady states of (27).

Proposition 5. *Assume that*

$$\begin{cases} K_\mu(r) < K < K_0(r), \\ r_\mu \leq r < r_\infty, \end{cases} \quad \textit{or} \quad \begin{cases} 0 \leq K < K_0(r), \\ 0 \leq r < r_\mu. \end{cases} \tag{35}$$

Then, (27) *has two distinct steady states:* 0 *and* $N^\star$ *given explicitly by (34). If* (35) *does not hold, then* 0 *is the only equilibrium of* (27).

Our objective is to show the existence of traveling wave front solutions for the coupled reaction-diffusion and difference equation (8). To this ends, a monotone iteration scheme will be established for the corresponding wave equation. Except for a few details, a similar technique was used in [32, 43]. Due to Proposition 4, we can reduce our study to the existence of bounded and monotone solutions of (27)-(30). We will use the classical method based on the notion of upper and lower solutions. Firstly, define the function $F : X^+ \longrightarrow C(\mathbb{R}, \mathbb{R})$, by

$$F(\phi)(z) = -f(\phi(z)) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left(\chi * g(\phi)\right)(z), \quad z \in \mathbb{R}, \quad \phi \in X^+.$$

Next, we show that $F(\phi)$ satisfies the quasi-monotonicity condition given in the following lemma.

Lemma 3. *Assume that* (1), (2), (17), (31) *and* (35) *hold. Then, there exists $B \geq 0$ such that F satisfies the following property*

$$F(\phi_1)(z) - F(\phi_2)(z) + B[\phi_1(z) - \phi_2(z)] \geq 0,$$

for all $\phi_1, \phi_2 \in X^+$ such that $0 \leq \phi_2(z) \leq \phi_1(z) \leq N^\star$, for all $z \in \mathbb{R}$.

Proof. We have

$$\begin{aligned} F(\phi_1)(z) - F(\phi_2)(z) &= -f(\phi_1(z)) + f(\phi_2(z)) \\ &\quad + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left(\chi * (g(\phi_1) - g(\phi_2))\right)(z). \end{aligned}$$

As $0 \leq \phi_2(z) \leq \phi_1(z) \leq N^\star$, then using (31) we obtain $\chi * (g(\phi_1) - g(\phi_2))(z) \geq 0$. Thus,

$$F(\phi_1)(z) - F(\phi_2)(z) \geq -f(\phi_1(z)) + f(\phi_2(z)).$$

Set

$$B = \sup\{f'(v) : v \in [0, N^\star]\} \geq 0. \tag{36}$$

We have

$$f(\phi_1(z)) - f(\phi_2(z)) \leq B\left[\phi_1(z) - \phi_2(z)\right].$$

We conclude that

$$F(\phi_1)(z) - F(\phi_2)(z) + B[\phi_1(z) - \phi_2(z)] \geq 0.$$

□

We define the profile set of traveling wave fronts as

$$\Gamma = \left\{ \begin{array}{ll} & \phi \in X^+ : \\ (i) & \phi(z) \text{ is non-decreasing on } \mathbb{R}, \\ (ii) & \lim_{z\to-\infty} \phi(z) = 0, \ \lim_{z\to+\infty} \phi(z) = N^\star \end{array} \right\}.$$

Consider the function $H : X^+ \longrightarrow C(\mathbb{R}, \mathbb{R})$ defined by

$$H(\phi)(z) = B\phi(z) + F(\phi)(z), \quad z \in \mathbb{R},$$

where B is given by (36). It is not difficult to prove the following properties of H.

Proposition 6. (i) *Let $\phi_1, \phi_2 \in X^+$, such that $0 \le \phi_1(z) \le \phi_2(z) \le N^\star$, for all $z \in \mathbb{R}$. Then, $0 \le H(\phi_1)(z) \le H(\phi_2)(z)$, for all $z \in \mathbb{R}$.*

(ii) *Let $\phi \in \Gamma$. Then, the function $z \to H(\phi)(z)$ is non-decreasing on $\mathbb{R}$ and satisfies $\lim_{z\to-\infty} H(\phi)(z) = 0$ and $\lim_{z\to+\infty} H(\phi)(z) = BN^\star$.*

Proof. (i) is a direct consequence of Lemma 3.
(ii) Let $\phi \in \Gamma$. To prove that the function $z \to H(\phi)(z)$ is non-decreasing on $\mathbb{R}$, we take $z \in \mathbb{R}$ and $y > 0$. Then, $0 \le \phi(z) \le \phi(z+y) \le N^\star$. We apply (i), hence $0 \le H(\phi)(z) \le H(\phi)(z+y)$. Then, $z \to H(\phi)(z)$ is non-decreasing on $\mathbb{R}$. Thanks to monotone convergence theorem, we have $\lim_{z\to-\infty} H(\phi)(z) = 0$ and $\lim_{z\to+\infty} H(\phi)(z) = BN^\star$. This finishes the proof. □

We add the following definition about upper and lower solutions of (20).

Definition 2. *A couple of continuous functions $(\overline{\phi}, \overline{\psi})$ (respectively, $(\underline{\phi}, \underline{\psi})$) is called an upper (respectively, lower) solution of (20) if $\overline{\phi}'$ and $\overline{\phi}''$ (respectively, $\underline{\phi}'$ and $\underline{\phi}''$) exist almost everywhere (a.e.) and they are essentially bounded on $\mathbb{R}$, and if $(\overline{\phi}, \overline{\psi})$ (respectively, $(\underline{\phi}, \underline{\psi})$) satisfies a.e. in $\mathbb{R}$, the inequalities*

$$\left\{ \begin{array}{l} c\overline{\phi}'(z) \ge d_1\overline{\phi}''(z) - f(\overline{\phi}(z)) + 2(1-K)e^{-\gamma r} \left(T_2(r)\overline{\psi}\right)(z - cr), \\ \overline{\psi}(z) \ge \beta(\underline{\phi}(z))\overline{\phi}(z) + 2Ke^{-\gamma r} \left(T_2(r)\overline{\psi}\right)(z - cr), \end{array} \right.$$

(respectively,

$$\left\{ \begin{array}{l} c\underline{\phi}'(z) \le d_1\underline{\phi}''(z) - f(\underline{\phi}(z)) + 2(1-K)e^{-\gamma r} \left(T_2(r)\underline{\psi}\right)(z - cr), \\ \underline{\psi}(z) \le \beta(\overline{\phi}(z))\underline{\phi}(z) + 2Ke^{-\gamma r} \left(T_2(r)\underline{\psi}\right)(z - cr)). \end{array} \right.$$

It is not difficult to prove that under the conditions (1) and (17), $\overline{\phi}$ and $\underline{\phi}$ satisfy the inequalities

$$c\overline{\phi}'(z) \geq d_1\overline{\phi}''(z) - f(\overline{\phi}(z)) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\overline{\phi})\right)(z), \quad \text{a.e. in } \mathbb{R}, \tag{37}$$

and

$$c\underline{\phi}'(z) \leq d_1\underline{\phi}''(z) - f(\underline{\phi}(z)) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\underline{\phi})\right)(z), \quad \text{a.e. in } \mathbb{R}. \tag{38}$$

The solutions $\overline{\phi}$ of (37) and $\underline{\phi}$ of (38) will be called respectively upper and lower solutions of (27). We assume that $\overline{\phi} \in \Gamma$ and $\underline{\phi}$ (which is not necessarily in Γ) exist and satisfy the following hypotheses,

(i) $0 \leq \underline{\phi}(z) \leq \overline{\phi}(z) \leq N^\star$, for all $z \in \mathbb{R}$,
(ii) $\underline{\phi} \not\equiv 0$.

Then, consider the following iteration scheme, for $z \in \mathbb{R}$,

$$\begin{cases} c\phi_n'(z) = d_1\phi_n''(z) - B\phi_n(z) + H(\phi_{n-1})(z), & n = 1, 2, \dots, \\ \underline{\phi}(z) \leq \phi_0(z) = \overline{\phi}(z). \end{cases} \tag{39}$$

Using a technique introduced in [43], we solve (39). Then, we obtain

$$\begin{cases} \phi_n(z) = \dfrac{1}{d_1(\alpha^+ - \alpha^-)}\left[\displaystyle\int_{-\infty}^{z} e^{\alpha^-(z-s)}H(\phi_{n-1})(s)\mathrm{d}s + \int_{z}^{+\infty} e^{\alpha^+(z-s)}H(\phi_{n-1})(s)\mathrm{d}s\right], \\ \phi_0(z) = \overline{\phi}(z), \end{cases}$$

with

$$\alpha^- = \frac{c}{2d_1}\left(1 - \sqrt{1 + \frac{4Bd_1}{c^2}}\right) < 0 \qquad \text{and} \qquad \alpha^+ = \frac{c}{2d_1}\left(1 + \sqrt{1 + \frac{4Bd_1}{c^2}}\right) > 0,$$

and $B \geq 0$ is given by (36).

Theorem 2. *Assume that* (1), (2), (17), (31) *and* (35) *hold. The function* ϕ_n *satisfies the following properties.*

(i) ϕ_n *solves the scheme* (39),
(ii) $\phi_n \in \Gamma$,
(iii) $\underline{\phi}(z) \leq \phi_n(z) \leq \phi_{n-1}(z) \leq \overline{\phi}(z)$, *for all* $z \in \mathbb{R}$,
(iv) *Each* ϕ_n *is an upper solution of* (27),

(v) $\phi(z) = \lim\limits_{n\to+\infty} \phi_n(z)$ *is a non-decreasing solution of* (27) *and satisfies*

$$\phi(-\infty) = 0, \quad \phi(+\infty) = N^\star.$$

Proof. The proof of this result is similar to the proof of the corresponding result in [43]. □

The last theorem gives us tools to construct solutions of (27)-(30), and then traveling fronts for the problem (8). First, we have to design suitable upper $\overline{\phi}$ and lower $\underline{\phi}$ solutions of (27). For $\lambda \in (0, \lambda^+(c))$ with $\lambda^+(c)$ defined by (28), let consider the following function

$$\Delta_c(\lambda) = -d_1\lambda^2 + c\lambda + \delta_0 + \beta_0 - \frac{2(1-K)\beta_0 e^{-\gamma r} e^{d_2 r\lambda^2 - cr\lambda}}{1 - 2Ke^{-\gamma r} e^{d_2 r\lambda^2 - cr\lambda}}, \tag{40}$$

with $\beta_0 := \beta(0)$ and $\delta_0 := \delta(0)$. It seems that $\lim\limits_{\lambda\to\lambda^+(c)} \Delta_c(\lambda) = -\infty$. We remark that $\Delta_c(\lambda)$ is transcendental characteristic function for the linearized problem of (27) near the zero solution. We put

$$\begin{cases} p(\lambda) = -d_1\lambda^2 + c\lambda + \delta_0 + \beta_0, \\ q(\lambda) = 1 - 2Ke^{-\gamma r} e^{d_2 r\lambda^2 - cr\lambda}, \\ l(\lambda) = 2(1-K)\beta_0 e^{-\gamma r} e^{d_2 r\lambda^2 - cr\lambda}. \end{cases}$$

Then the expression (40) can be written as

$$\Delta_c(\lambda) = p(\lambda) - \frac{l(\lambda)}{q(\lambda)}, \quad \lambda \in \left(0, \lambda^+(c)\right).$$

It is not difficult to see that

$$\Delta_c(0) = \frac{\delta_0(1 - 2Ke^{-\gamma r}) - \beta_0(2e^{-\gamma r} - 1)}{1 - 2Ke^{-\gamma r}} < 0.$$

Next, for $c > 0$ and $\lambda \in [0, \lambda^+(c))$,

$$\frac{\partial}{\partial\lambda}\Delta_c(\lambda) = \frac{(c - 2d_1\lambda)q^2(\lambda) + (c - 2d_2\lambda)rl(\lambda)}{q^2(\lambda)}. \tag{41}$$

We put

$$\underline{\lambda}(c) := \frac{c}{2}\min\left\{\frac{1}{d_1}, \frac{1}{d_2}\right\} \quad \text{and} \quad \overline{\lambda}(c) := \min\left\{\frac{c}{2}\max\left\{\frac{1}{d_1}, \frac{1}{d_2}\right\}, \lambda^+(c)\right\}.$$

It is easy to prove that $0 < \underline{\lambda}(c) \leq \overline{\lambda}(c) \leq \lambda^+(c)$ and

$$\left(\frac{\partial}{\partial \lambda} \Delta_c(\lambda) \big|_{\lambda = \underline{\lambda}(c)} \right) \left(\lim_{\lambda \to \overline{\lambda}(c)} \frac{\partial}{\partial \lambda} \Delta_c(\lambda) \right) < 0.$$

Furthermore, the second derivative of the function $\lambda \mapsto \Delta_c(\lambda)$ is given, for all $\lambda \in [0, \lambda^+(c))$, by

$$\begin{aligned} \frac{\partial^2}{\partial \lambda^2} \Delta_c(\lambda) &= -\frac{2d_1 q^4(\lambda) + 2d_2 r l(\lambda) q^2(\lambda) + (c - 2d_2\lambda)^2 r^2 l(\lambda) q^2(\lambda)}{q^4(\lambda)} \\ &\quad - \frac{r^2 l(\lambda) q(\lambda)(c - 2d_2\lambda)^2 (2 - q(\lambda))}{q^4(\lambda)} < 0. \end{aligned} \tag{42}$$

Then, for each $c > 0$ and $d_1 \neq d_2$, there exists a unique $\lambda^\star(c) \in \left(\underline{\lambda}(c), \overline{\lambda}(c)\right)$ such that

$$\frac{\partial}{\partial \lambda} \Delta_c(\lambda) \big|_{\lambda = \lambda^\star(c)} = 0. \tag{43}$$

Moreover, by (41) we have

$$\frac{\partial}{\partial c} \left(\frac{\partial}{\partial \lambda} \Delta_c(\lambda) \right) = 1 + \frac{\left[\bar{l}(c) + (c - 2d_2\lambda) \bar{l}'(c) \right] r \overline{q}^2(c) - 2r(c - 2d_2\lambda) \bar{l}(c) \overline{q}'(c) \overline{q}(c)}{\overline{q}^4(c)}, \tag{44}$$

with

$$\bar{l}(c) = 2(1 - K)\beta_0 e^{-\gamma r} e^{d_2 r \lambda^2 - c r \lambda} \quad \text{and} \quad \overline{q}(c) = 1 - 2K e^{-\gamma r} e^{d_2 r \lambda^2 - c r \lambda}.$$

It is clear that $\bar{l}'(c) < 0$, $\overline{q}'(c) > 0$ and $c - 2d_2\lambda < 0$, for $c > 0$ and $\lambda \in [0, \lambda^+(c))$. Then, we conclude from (42) and (44) that

$$\frac{\partial^2}{\partial \lambda^2} \Delta_c(\lambda) < 0 \quad \text{and} \quad \frac{\partial}{\partial c} \left(\frac{\partial}{\partial \lambda} \Delta_c(\lambda) \right) > 0, \quad \text{for all } c > 0 \text{ and } \lambda \in [0, \lambda^+(c)).$$

Thus, using the implicit function theorem, one can conclude that the function $c \mapsto \lambda^\star(c)$ is strictly increasing on $(0, +\infty)$ with $\lim_{c \to 0} \lambda^\star(c) = 0$ and $\lim_{c \to +\infty} \lambda^\star(c) = +\infty$. Consider the function $c \mapsto \Delta_c(\lambda^\star(c))$ defined on $(0, +\infty)$. We have

$$\frac{\mathrm{d}}{\mathrm{d}c} \left[\Delta_c(\lambda^\star(c)) \right] = \frac{\partial}{\partial c} \Delta_c(\lambda^\star(c)) + \left[\frac{\partial}{\partial \lambda} \Delta_c(\lambda) \big|_{\lambda = \lambda^\star(c)} \right] \times \left[\frac{\mathrm{d}}{\mathrm{d}c} \lambda^\star(c) \right].$$

Thanks to (43), we obtain

$$\frac{\mathrm{d}}{\mathrm{d}c} \left[\Delta_c(\lambda^\star(c)) \right] = \frac{\partial}{\partial c} \Delta_c(\lambda^\star(c)).$$

Then,

$$\frac{\mathrm{d}}{\mathrm{d}c}\left[\Delta_c\left(\lambda^\star(c)\right)\right] = \lambda^\star(c)\left[1 + \frac{rl(\lambda^\star(c))\left(q(\lambda^\star(c)) + 2Ke^{-\gamma r}e^{d_2 r(\lambda^\star(c))^2 - cr\lambda^\star(c)}\right)}{q^2(\lambda^\star(c))}\right] > 0.$$

Moreover,

$$\lim_{c\to 0}\Delta_c\left(\lambda^\star(c)\right) = \delta_0 + \beta_0 - \frac{2(1-K)\beta_0 e^{-\gamma r}}{1-2Ke^{-\gamma r}} < 0,$$

and

$$\Delta_c\left(\lambda^\star(c)\right) \geq \Delta_c\left(\underline{\lambda}(c)\right) \quad \text{with} \quad \lim_{c\to+\infty}\Delta_c\left(\underline{\lambda}(c)\right) = +\infty.$$

We conclude that there exists a unique $c^\star > 0$ such that

$$\begin{cases} \Delta_{c^\star}(\lambda^\star(c^\star)) = 0, \\ \dfrac{\partial}{\partial\lambda}\Delta_{c^\star}(\lambda)\big|_{\lambda=\lambda^\star(c^\star)} = 0. \end{cases}$$

Remark that if $d_1 = d_2 := d$, we have $\lambda^\star(c) = \underline{\lambda}(c) = \overline{\lambda}(c) = \dfrac{c}{2d} < \lambda^+(c)$. Furthermore, $c^\star$ is given explicitly by

$$c^\star = 2\sqrt{dG^{-1}\left(2(1-K)\beta_0 e^{-\gamma r}\right)},$$

where the function G is given, for $x \geq 0$, by $G(x) = (x + \delta_0 + \beta_0)\left(e^{rx} - 2Ke^{-\gamma r}\right)$. We have proved the following result.

Lemma 4. *Assume that* (17) *and* (35) *hold. Then, there exists a unique* $c^\star > 0$ *and for each* $c > 0$ *there exists a unique* $\lambda^\star(c) \in \left[\underline{\lambda}(c), \overline{\lambda}(c)\right]$ *such that*

(i) *if* $c = c^\star$, $\Delta_{c^\star}(\lambda^\star(c^\star)) = \dfrac{\partial}{\partial\lambda}\Delta_{c^\star}(\lambda)\big|_{\lambda=\lambda^\star(c^\star)} = 0$,

(ii) *if* $c > c^\star$, *there exist two real roots,* $\lambda_1(c)$ *and* $\lambda_2(c)$, *of the equation* $\Delta_c(\lambda) = 0$ *such that* $0 < \lambda_1(c) < \lambda^\star(c) < \lambda_2(c) < \lambda^+(c)$ *and* $\Delta_c(\lambda) > 0$ *for all* $\lambda \in (\lambda_1(c), \lambda_2(c))$,

(iii) *if* $0 < c < c^\star$, $\Delta_c(\lambda) < 0$ *for all* $\lambda \in (0, \lambda^+(c))$.

Now, we are in position to construct upper and lower solutions of (27). We fix $c > c^\star$ and we put $\lambda_1 := \lambda_1(c)$, $\lambda_2 := \lambda_2(c)$, with $c^\star$, $\lambda_1(c)$ and $\lambda_2(c)$ defined in Lemma 4. We need the following assumption.

$$\beta(N) + \delta(N) \geq \beta(0) + \delta(0), \text{ for all } N \in [0, N^\star], \tag{45}$$

where $N^\star$ is the positive steady state of (27).

Lemma 5. *Assume that* (1), (2), (17), (31), (35) *and* (45) *hold and let* $c > c^\star$ *be fixed. Then, the following properties hold.*

1. *The function* $\overline{\phi} : \mathbb{R} \to \mathbb{R}^+$ *defined by* $\overline{\phi}(t) = \min\{N^\star, e^{\lambda_1 t}\}$ *is an upper solution of* (27) *belonging to* Γ.
2. *The function* $\underline{\phi} : \mathbb{R} \to \mathbb{R}^+$ *defined by* $\underline{\phi}(t) = \max\{0, e^{\lambda_1 t} - Me^{\omega\lambda_1 t}\}$, *with* $\omega \in (1, \min\{2, \lambda_2/\lambda_1\})$ *and* $M > 1$ *well-chosen, is a lower solution of* (27).
3. $\underline{\phi}(t) \leq \overline{\phi}(t)$, *for all* $t \in \mathbb{R}$.

Proof. As $\lambda_1 > 0$ there exists $t_1 \in \mathbb{R}$ such that

$$\overline{\phi}(t) = \begin{cases} N^\star, & t \geq t_1, \\ e^{\lambda_1 t}, & t < t_1. \end{cases}$$

We can choose $t_1 := \dfrac{1}{\lambda_1} \ln(N^\star)$. Then, it is clear that $\overline{\phi} \in \Gamma$. Suppose that $t \in [t_1, +\infty)$. Then, $\overline{\phi}(t) = N^\star$, $\overline{\phi}'(t) = \overline{\phi}''(t) = 0$ and as g is an increasing function on $[0, N^\star]$, we have by the point (2) of Lemma 2,

$$\left(\chi * g(\overline{\phi})\right)(t) \leq \left(\chi * g(N^\star)\right)(t) = g(N^\star).$$

Then, we obtain

$$\begin{aligned} c\overline{\phi}'(t) - d_1\overline{\phi}''(t) + f(\overline{\phi}(t)) - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left(\chi * g(\overline{\phi})\right)(t) \\ \geq f(N^\star) - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} g(N^\star) = 0. \end{aligned}$$

Suppose that $t \in (-\infty, t_1)$. Then, $\overline{\phi}(t) = e^{\lambda_1 t}$. Consequently,

$$c\overline{\phi}'(t) - d_1\overline{\phi}''(t) = \left(c\lambda_1 - d_1\lambda_1^2\right) e^{\lambda_1 t},$$

and, due to (45)

$$f(\overline{\phi}(t)) := \left(\delta(\overline{\phi}(t)) + \beta(\overline{\phi}(t))\right)\overline{\phi}(t) \geq (\delta(0) + \beta(0))\overline{\phi}(t) = (\delta_0 + \beta_0)e^{\lambda_1 t}.$$

Furthermore, by (1) and the point (3) of Lemma 2

$$\left(\chi * g(\overline{\phi})\right)(t) \leq \beta_0 \left(\chi * \overline{\phi}\right)(t) \leq \beta_0 \left(\chi * e^{\lambda_1 \cdot}\right)(t) = \frac{\left(1 - 2Ke^{-\gamma r}\right)\beta_0 e^{d_2 r\lambda_1^2 + (t-cr)\lambda_1}}{1 - 2Ke^{-\gamma r}e^{d_2 r\lambda_1^2 - cr\lambda_1}}.$$

Then,

$$c\overline{\phi}'(t) - d_1\overline{\phi}''(t) + f(\overline{\phi}(t)) - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left(\chi * g(\overline{\phi})\right)(t) \geq \Delta_c(\lambda_1)e^{\lambda_1 t} = 0.$$

Let $\nu \in (\omega - 1, \min\{2, \lambda_2/\lambda_1\} - 1)$. It is clear that $0 < \nu < 1$. Recall that β is decreasing and $\beta(N) + \delta(N) \geq \beta_0 + \delta_0$ for $N \in [0, N^\star]$. Then, under the assumption $\beta,\ \delta \in C^1([0, N^\star])$, there exists a number $\overline{\alpha} > 0$ such that

$$\beta_0 - \beta(u) \leq \overline{\alpha} u^\nu \quad \text{and} \quad \delta(u) + \beta(u) - (\delta_0 + \beta_0) \leq \overline{\alpha} u^\nu, \quad \text{for } u \in [0, N^\star].$$

We will construct a lower solution $\underline{\phi}$ of the form

$$\underline{\phi}(t) = \begin{cases} e^{\lambda_1 t} - M e^{\omega \lambda_1 t}, & t < t_2, \\ 0, & t \geq t_2, \end{cases}$$

with

$$t_2 := \frac{1}{(\omega - 1)\lambda_1} \ln\left(\frac{1}{M}\right),$$

and $M > 1$ is a constant. Then, $t_2 < 0$. First, remark that to get $\underline{\phi} \leq \overline{\phi}$, it suffices to choose $M > (N^\star)^{1-\omega}$.

Let $t \in [t_2, +\infty)$. Then, $\underline{\phi}(t) = 0$. Thus,

$$c\underline{\phi}'(t) - d_1\underline{\phi}''(t) + f(\underline{\phi}(t)) - \frac{2(1-K)e^{-\gamma r}}{1 - 2Ke^{-\gamma r}} \left(\chi * g(\underline{\phi})\right)(t) = -\frac{2(1-K)e^{-\gamma r}}{1 - 2Ke^{-\gamma r}} \left(\chi * g(\underline{\phi})\right)(t).$$

The function $\underline{\phi}$ is nonnegative on $\mathbb{R}$. Then, $\chi * g(\underline{\phi})$ is also nonnegative on $\mathbb{R}$. We conclude that

$$c\underline{\phi}'(t) - d_1\underline{\phi}''(t) + f(\underline{\phi}(t)) - \frac{2(1-K)e^{-\gamma r}}{1 - 2Ke^{-\gamma r}} \left(\chi * g(\underline{\phi})\right)(t) \leq 0, \quad \text{for all } t \in [t_2, +\infty).$$

Let $t \in (-\infty, t_2)$. We have $\underline{\phi}(t) = e^{\lambda_1 t} - M e^{\omega \lambda_1 t}$. Then,

$$c\underline{\phi}'(t) - d_1\underline{\phi}''(t) = c\lambda_1 e^{\lambda_1 t} - cM\omega\lambda_1 e^{\omega\lambda_1 t} - d_1\lambda_1^2 e^{\lambda_1 t} + d_1 M \omega^2 \lambda_1^2 e^{\omega\lambda_1 t}.$$

Thanks to $\Delta_c(\lambda_1) = 0$, we obtain

$$\begin{aligned} c\underline{\phi}'(t) - d_1\underline{\phi}''(t) &= \frac{l(\lambda_1)}{q(\lambda_1)} e^{\lambda_1 t} - (\delta_0 + \beta_0) e^{\lambda_1 t} - \Delta_c(\omega\lambda_1) M e^{\omega\lambda_1 t} \\ &\quad - \frac{l(\omega\lambda_1)}{q(\omega\lambda_1)} M e^{\omega\lambda_1 t} + (\delta_0 + \beta_0) M e^{\omega\lambda_1 t}, \end{aligned}$$

and,

$$\begin{aligned} f(\underline{\phi}(t)) - (\delta_0 + \beta_0)\left(e^{\lambda_1 t} - M e^{\omega\lambda_1 t}\right) &= (\delta(\underline{\phi}(t)) + \beta(\underline{\phi}(t)))\underline{\phi}(t) - (\delta_0 + \beta_0)\,\underline{\phi}(t), \\ &\leq \overline{\alpha}\underline{\phi}^{(\nu+1)}(t). \end{aligned}$$

Furthermore, due to (28), we have

$$1-2Ke^{-\gamma r}e^{d_2 r\lambda_1^2-cr\lambda_1}>0. \tag{46}$$

Then, we can write

$$\begin{aligned}\frac{l(\lambda_1)}{q(\lambda_1)}e^{\lambda_1 t} &= 2(1-K)e^{-\gamma r}\beta_0\frac{e^{d_2 r\lambda_1^2+(t-cr)\lambda_1}}{1-2Ke^{-\gamma r}e^{d_2 r\lambda_1^2-cr\lambda_1}},\\ &= \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta_0\left(\chi * e^{\lambda_1 \cdot}\right)(t).\end{aligned}$$

We know that $\omega\in(1,\min\{2,\lambda_2/\lambda_1\})$, then

$$\Delta_c(\omega\lambda_1)>0 \quad \text{and} \quad 1-2Ke^{-\gamma r}e^{d_2 r\omega^2\lambda_1^2-cr\omega\lambda_1}>0.$$

Hence, as $\omega\lambda_1<\lambda^+(c)$, we have

$$\frac{l(\omega\lambda_1)}{q(\omega\lambda_1)}e^{\omega\lambda_1 t}=\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta_0\left(\chi * e^{\omega\lambda_1 \cdot}\right)(t).$$

Consequently,

$$\frac{l(\lambda_1)}{q(\lambda_1)}e^{\lambda_1 t}-\frac{l(\omega\lambda_1)}{q(\omega\lambda_1)}Me^{\omega\lambda_1 t}\leq \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta_0\left(\chi * \underline{\phi}\right)(t).$$

We conclude that

$$\begin{aligned}c\underline{\phi}'(t)-d_1\underline{\phi}''(t)+f(\underline{\phi}(t)) &\leq -\Delta_c(\omega\lambda_1)Me^{\omega\lambda_1 t}+\overline{\alpha}\underline{\phi}^{(\nu+1)}(t)\\ &\quad +\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta_0\left(\chi * \underline{\phi}\right)(t),\end{aligned}$$

and

$$\beta_0\left(\chi * \underline{\phi}\right)(t)-\left(\chi * g(\underline{\phi})\right)(t)=\left(\chi * \left(\beta_0-\beta(\underline{\phi})\right)\underline{\phi}\right)(t)\leq \overline{\alpha}\left(\chi * \underline{\phi}^{(\nu+1)}\right)(t).$$

It is not difficult to see that

$$\underline{\phi}^{(\nu+1)}(s)\leq e^{(\nu+1)\lambda_1 s}, \quad \text{for all } s\in\mathbb{R}.$$

Then,

$$\begin{aligned}&c\underline{\phi}'(t)-d_1\underline{\phi}''(t)+f(\underline{\phi}(t))-\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\underline{\phi})\right)(t)\\ &\qquad \leq -\Delta_c(\omega\lambda_1)Me^{\omega\lambda_1 t}+\overline{\alpha}e^{(\nu+1)\lambda_1 t}+\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\overline{\alpha}\left(\chi * e^{(\nu+1)\lambda_1 \cdot}\right)(t).\end{aligned}$$

Thanks to (29), we have

$$\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\overline{\alpha}\left(\chi * e^{(\nu+1)\lambda_1 \cdot}\right)(t) = \frac{\overline{\alpha} l((\nu+1)\lambda_1)}{\beta_0 q((\nu+1)\lambda_1)} e^{(\nu+1)\lambda_1 t}.$$

Then,

$$\overline{\alpha} e^{(\nu+1)\lambda_1 t} + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\overline{\alpha}\left(\chi * e^{(\nu+1)\lambda_1 \cdot}\right)(t) = \overline{\alpha} e^{(\nu+1)\lambda_1 t}\left[1 + \frac{l((\nu+1)\lambda_1)}{\beta_0 q((\nu+1)\lambda_1)}\right].$$

Thus,

$$\begin{aligned} &c\underline{\phi}'(t) - d_1\underline{\phi}''(t) + f(\underline{\phi}(t)) - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\underline{\phi})\right)(t) \\ &\qquad \le e^{\omega\lambda_1 t}\left[-\Delta_c(\omega\lambda_1)M + \overline{\alpha} e^{(\nu+1-\omega)\lambda_1 t}\left(1 + \frac{l((\nu+1)\lambda_1)}{\beta_0 q((\nu+1)\lambda_1)}\right)\right]. \end{aligned}$$

Remember that $\nu + 1 - \omega > 0$, $\lambda_1 > 0$ and $t_2 < 0$. So, $e^{(\nu+1-\omega)\lambda_1 t} < 1$, for all $t < t_2$. Then, for $t < t_2$,

$$\begin{aligned} &c\underline{\phi}'(t) - d_1\underline{\phi}''(t) + f(\underline{\phi}(t)) - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\underline{\phi})\right)(t) \\ &\qquad \le e^{\omega\lambda_1 t}\left[-\Delta_c(\omega\lambda_1)M + \overline{\alpha}\left(1 + \frac{l((\nu+1)\lambda_1)}{\beta_0 q((\nu+1)\lambda_1)}\right)\right]. \end{aligned}$$

Finally, we can choose

$$M > \max\left\{1, (N^\star)^{\omega+1}, \overline{\alpha}\left(1 + \frac{l((\nu+1)\lambda_1)}{\beta_0 q((\nu+1)\lambda_1)}\right)(\Delta_c(\omega\lambda_1))^{-1}\right\}.$$

The proof is completed. □

We can thus formulate the following theorem for the existence of monotone solutions of the problem (27) with $\phi(-\infty) = 0$ and $\phi(+\infty) = N^\star$.

Theorem 3. *Assume that* (1), (2), (17), (31), (35) *and* (45) *hold. Then, for every* $c > c^\star$, (27) *has a solution in* Γ. *Therefore,* (8) *has a traveling wave front which connects* 0 *to the positive equilibrium* $N^\star$.

Proof. Let $c > c^\star$. The proof of this theorem follows directly from Theorem 2 and Lemma 5. □

Theorem 4. *Assume that* (1), (2), (17), (31), (35) *and* (45) *hold and* $c = c^\star$. *Then,* (27) *has a solution in* Γ. *Therefore,* (8) *has a traveling wave front which connects* 0 *to the positive equilibrium* $N^\star$.

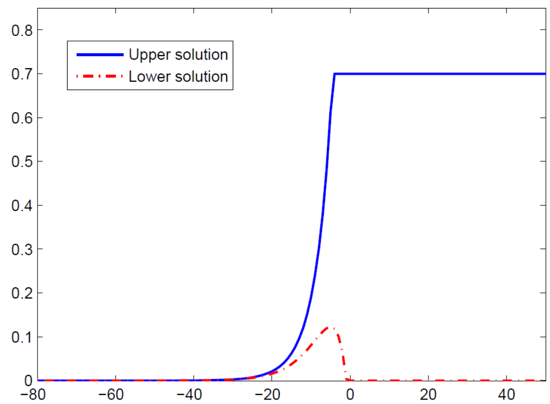

Figure 2: The shapes of the upper solution $\overline{\phi}$ and the lower solution $\underline{\phi}$ are represented.

Proof. Let $c = c^\star$. We use some ideas developed in [14, 35, 44, 45]. We consider a sequence $(c_m)_{m\geq 1} \subseteq (c^\star, +\infty)$ such that $\lim_{m\to+\infty} c_m = c^\star$. For instance, we can choose $c_m = c^\star + 1/m$. It follows from Theorem 3 that for $c = c_m > c^\star$, (27) has a solution in Γ. We denote by ϕ_m this solution. It is clear that ϕ_m is invariant with respect to spatial translation. This means that, for each $m \geq 1$ and each $a \in \mathbb{R}$, the function $\phi_{a,m}(\cdot) := \phi_m(\cdot + a)$ satisfies (27) and it belongs to Γ. Furthermore, $\lim_{a\to-\infty} \phi_{a,m}(0) = \lim_{a\to-\infty} \phi_m(a) = 0$ and $\lim_{a\to+\infty} \phi_{a,m}(0) = \lim_{a\to+\infty} \phi_m(a) = N^\star$. Then, for each $m \geq 1$, we can choose $a_m \in \mathbb{R}$ such that $\phi_{a_m,m}(0) = N^\star/2$. Furthermore, within the notation used in (39), $\phi_{a_m,m}$ is given by

$$\begin{aligned}\phi_{a_m,m}(z) = \quad & \frac{1}{d_1(\alpha_{2,m} - \alpha_{1,m})} \left[\int_{-\infty}^{z+a_m} e^{\alpha_{1,m}(z+a_m-s)} H(\phi_{a_m,m})(s)\mathrm{d}s \right. \\ & \left. + \int_{z+a_m}^{+\infty} e^{\alpha_{2,m}(z+a_m-s)} H(\phi_{a_m,m})(s)\mathrm{d}s \right],\end{aligned} \tag{47}$$

where $\alpha_{1,m}, \alpha_{2,m}$ are given by

$$\alpha_{1,m} = \frac{1}{2d_1}\left(c_m - \sqrt{c_m^2 + 4Bd_1}\right) < 0 \quad \text{and} \quad \alpha_{2,m} = \frac{1}{2d_1}\left(c_m + \sqrt{c_m^2 + 4Bd_1}\right) > 0.$$

We verify the boundedness of $\phi'_{a_m,m}$ on $\mathbb{R}$. In fact, if we differentiate (47) with respect to z, we get

$$\phi'_{a_m,m}(z) = \frac{1}{d_1(\alpha_{2,m}-\alpha_{1,m})}\left[\int_{-\infty}^{z+a_m} \alpha_{1,m}e^{\alpha_{1,m}(z+a_m-s)}H(\phi_{a_m,m})(s)\mathrm{d}s \right. \\ \left. + \int_{z+a_m}^{+\infty} \alpha_{2,m}e^{\alpha_{2,m}(z+a_m-s)}H(\phi_{a_m,m})(s)\mathrm{d}s\right].$$

Therefore $|\phi'_{a_m,m}(z)| \leq b_1$, for all $z \in \mathbb{R}$ and by (27), we obtain $|\phi''_{a_m,m}(z)| \leq b_2$, for all $z \in \mathbb{R}$. Differentiating both sides of (27) with respect to z, we get

$$d_1\phi'''_{a_m,m}(z) = c_m\phi''_{a_m,m}(z) + \left[\delta(\phi_{a_m,m}(z)) + \beta(\phi_{a_m,m}(z))\right]\phi'_{a_m,m}(z) \\ + \left[\delta'(\phi_{a_m,m}(z)) + \beta'(\phi_{a_m,m}(z))\right]\phi'_{a_m,m}(z)\phi_{a_m,m}(z) \\ - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g'(\phi_{a_m,m})\phi'_{a_m,m}\right)(z).$$

It follows that $|\phi'''_{a_m,m}(z)| \leq b_3$, for all $z \in \mathbb{R}$. Consequently, $\phi_{a_m,m}$, $\phi'_{a_m,m}$ and $\phi''_{a_m,m}$ are uniformly bounded and equicontinuous sequences of functions on $\mathbb{R}$. By Ascoli's theorem there exists a subsequence of $(c_m)_{m\geq 1}$ (for simplicity, we preserve the same sequence $(c_m)_{m\geq 1}$), such that $\lim\limits_{m\to+\infty} c_m = c^\star$ and $\phi_{a_m,m}(z)$, $\phi'_{a_m,m}(z)$ and $\phi''_{a_m,m}(z)$ converge uniformly on every bounded interval. Then, they converge pointwise on $\mathbb{R}$ to $\phi(z)$, $\phi'(z)$ and $\phi''(z)$, respectively. Now, we pass to the limit in (27) and by using Lebesque's dominated convergence theorem for $(\chi * g(\phi_{a_m,m}))(z)$, we get

$$c^\star\phi'(z) = d_1\phi''(z) - f(\phi(z)) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\phi)\right)(z).$$

Then, ϕ is a solution of (27) with $c = c^\star$. It is not difficult to see that ϕ is nondecreasing on $\mathbb{R}$ and satisfies $\phi(0) = N^\star/2$, $0 \leq \phi(z) \leq N^\star$ for all $z \in \mathbb{R}$. Then, $\lim\limits_{z\to-\infty}\phi(z)$ and $\lim\limits_{z\to+\infty}\phi(z)$ exist. On the other hand, by differentiating both sides of the last equation with respect to z, we get $|\phi'''(z)| \leq b_3$, for all $z \in \mathbb{R}$. Consequently, $\phi'(\pm\infty) = \phi''(\pm\infty) = 0$. Moreover, the function $\phi \mapsto g(\phi) := \beta(\phi)\phi$ is increasing in $[0, N^\star]$. Then, by monotone convergence theorem and letting $z \to \pm\infty$, we obtain

$$(\delta(\phi(\pm\infty)) + \beta(\phi(\pm\infty)))\phi(\pm\infty) = \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta(\phi(\pm\infty))\phi(\pm\infty).$$

Then, by the fact that 0 and $N^\star$ are the unique steady states of (27) and $0 \leq \phi(-\infty) \leq N^\star/2 \leq \phi(+\infty) \leq N^\star$, we conclude that $\phi(-\infty) = 0$ and $\phi(+\infty) = N^\star$. As a consequence, we have that for $c = c^\star$, (27) has a solution in Γ. The proof is completed. $\square$

In the next results, we give some properties of the traveling wave fronts of (27).

Lemma 6. *Let ϕ be a traveling wave front of* (27) *connecting* 0 *to the positive equilibrium $N^\star$ and let $z \in \mathbb{R}$. Then, we have*

(i) $\displaystyle\int_{-\infty}^{z} |(\chi * \phi)(y) - \phi(y)|\mathrm{d}y < +\infty,$

(ii) $\displaystyle\varphi(z) := \int_{-\infty}^{z} \phi(y)\mathrm{d}y < +\infty,$

(iii) $\displaystyle\int_{-\infty}^{z} (\chi * \phi)(y)\mathrm{d}y = (\chi * \varphi)(z),$

(iv) $\displaystyle\int_{-\infty}^{z} |(\chi * \varphi)(y) - \varphi(y)|\mathrm{d}y < +\infty.$

Proof. (i) Let $t < z$. From the definition of convolution product, we obtain

$$\int_{t}^{z} [(\chi * \phi)(y) - \phi(y)]\mathrm{d}y = \int_{t}^{z} \left[\int_{-\infty}^{+\infty} \chi(s)\phi(y-s)\mathrm{d}s - \phi(y)\right] \mathrm{d}y,$$

and from Lemma 2, we have $\displaystyle\int_{-\infty}^{+\infty} \chi(s)\mathrm{d}s = 1$. Then,

$$\int_{t}^{z} \left[\int_{-\infty}^{+\infty} \chi(s)\phi(y-s)\mathrm{d}s - \phi(y)\right] \mathrm{d}y = \int_{t}^{z} \int_{-\infty}^{+\infty} \chi(s)[\phi(y-s) - \phi(y)]\mathrm{d}s\mathrm{d}y.$$

By using the fact that

$$\phi(y-s) - \phi(y) = -\int_{y-s}^{y} \phi'(x)\mathrm{d}x = -s\int_{0}^{1} \phi'(y-\eta s)\mathrm{d}\eta,$$

we get,

$$\int_{t}^{z} [(\chi * \phi)(y) - \phi(y)]\mathrm{d}y = -\int_{t}^{z} \int_{-\infty}^{+\infty} s\ \chi(s) \int_{0}^{1} \phi'(y-\eta s)\mathrm{d}\eta\mathrm{d}s\mathrm{d}y.$$

Fubini's theorem implies

$$\int_{t}^{z} [(\chi * \phi)(y) - \phi(y)]\mathrm{d}y = -\int_{-\infty}^{+\infty} s\ \chi(s) \int_{0}^{1} \int_{t}^{z} \phi'(y-\eta s)\mathrm{d}y\mathrm{d}\eta\mathrm{d}s.$$

Moreover, the dominated convergence theorem implies

$$\int_{-\infty}^{z} [(\chi * \phi)(y) - \phi(y)]\mathrm{d}y = -\int_{-\infty}^{+\infty} s\chi(s) \int_{0}^{1} \left[\lim_{t\to-\infty} \int_{t}^{z} \phi'(y-\eta s)\mathrm{d}y\right] \mathrm{d}\eta\mathrm{d}s.$$

Recall that $\lim_{x\to-\infty}\phi(x)=0$. Then, $\lim_{t\to-\infty}\int_t^z \phi'(y-\eta s)\mathrm{d}y=\phi(z-\eta s)$. This yields to

$$\int_{-\infty}^{z}[(\chi*\phi)(y)-\phi(y)]\mathrm{d}y=-\int_{-\infty}^{+\infty} y\chi(y)\int_0^1 \phi(z-\eta y)\mathrm{d}\eta\mathrm{d}y.$$

The function ϕ is bounded on $\mathbb{R}$. Then, $(y,z)\in\mathbb{R}\times\mathbb{R}\longmapsto\int_0^1\phi(z-\eta y)\mathrm{d}\eta$ is bounded. We have also $\int_{-\infty}^{+\infty}|y\ \chi(y)|\mathrm{d}y<+\infty$. We conclude, for $z\in\mathbb{R}$, that

$$\int_{-\infty}^{z}|(\chi*\phi)(y)-\phi(y)|\mathrm{d}y<+\infty.$$

(ii) Recall that the function ϕ is positive and satisfies

$$c\phi'(y)=d_1\phi''(y)-f(\phi(y))+\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi*g(\phi)\right)(y), \qquad (48)$$

with $\phi(-\infty)=0, \quad \phi(+\infty)=N^{\star}$. The continuity of β and δ implies that

$$\lim_{y\to-\infty}\beta(\phi(y))=\beta_0 \quad \text{and} \quad \lim_{y\to-\infty}\delta(\phi(y))+\beta(\phi(y))=\delta_0+\beta_0.$$

Then, for $\varepsilon>0$ small enough ($\varepsilon<\beta_0$), there exists $\overline{y}_\varepsilon<0$ such that, for all $y<\overline{y}_\varepsilon$, we have

$$\begin{cases}\beta_0-\varepsilon<\beta(\phi(y))\leq\beta_0+\varepsilon,\\ \delta_0+\beta_0-\varepsilon\leq\delta(\phi(y))+\beta(\phi(y))<\delta_0+\beta_0+\varepsilon.\end{cases}$$

Then, (48) implies, for $y<\overline{y}_\varepsilon$,

$$c\phi'(y)\geq d_1\phi''(y)-(\varepsilon+\delta_0+\beta_0)\phi(y)+\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)\left(\chi*\phi\right)(y). \quad (49)$$

Let us denote by

$$J_\varepsilon=\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)-(\varepsilon+\delta_0+\beta_0), \quad \text{with} \quad 0<\varepsilon<\beta_0.$$

We rewrite the inequality (49), for $y<\overline{y}_\varepsilon$, in the form

$$J_\varepsilon\phi(y)\leq c\phi'(y)-d_1\phi''(y)-\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)[\left(\chi*\phi\right)(y)-\phi(y)].$$

On the other hand, the condition for the existence of positive equilibrium can be written as

$$\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta_0 - (\delta_0 + \beta_0) > 0.$$

Then, we can choose $\varepsilon \in (0, \beta_0)$ small enough such that

$$\varepsilon \left(\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} + 1 \right) < \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta_0 - (\delta_0 + \beta_0).$$

Hence, J_ε is positive. As a consequence of (i), for $z < \overline{y}_\varepsilon$,

$$\begin{aligned} 0 \leq J_\varepsilon \int_{-\infty}^{z} \phi(y)\mathrm{d}y &\leq c\phi(z) - d_1\phi'(z) \\ &\quad - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0 - \varepsilon)\int_{-\infty}^{z} [(\chi * \phi)(y) - \phi(y)]\mathrm{d}y < +\infty. \end{aligned} \tag{50}$$

Then, for all $z \in \mathbb{R}$, $0 \leq \int_{-\infty}^{z} \phi(y)\mathrm{d}y < +\infty$.

(iii) Let $t < z$. Fubini's theorem implies that

$$\begin{aligned} \int_{t}^{z} (\chi * \phi)(y)\mathrm{d}y &= \int_{t}^{z}\int_{-\infty}^{+\infty} \chi(x)\phi(y-x)\mathrm{d}x\mathrm{d}y, \\ &= \int_{-\infty}^{+\infty} \chi(x)\int_{t}^{z} \phi(y-x)\mathrm{d}y\mathrm{d}x. \end{aligned}$$

By using the dominated convergence theorem, we obtain

$$\begin{aligned} \int_{-\infty}^{z} (\chi * \phi)(y)\mathrm{d}y &= \int_{-\infty}^{+\infty} \chi(x)\left[\lim_{t\to-\infty}\int_{t}^{z} \phi(y-x)\mathrm{d}y\right]\mathrm{d}x, \\ &= \int_{-\infty}^{+\infty} \chi(x)\int_{-\infty}^{z} \phi(y-x)\mathrm{d}y\mathrm{d}x, \\ &= \int_{-\infty}^{+\infty} \chi(x)\int_{-\infty}^{z-x} \phi(s)\mathrm{d}s\mathrm{d}x, \\ &= (\chi * \varphi)(z). \end{aligned}$$

(iv) We have, for $\varphi(y) := \int_{-\infty}^{y} \phi(x)\mathrm{d}x$,

$$\begin{aligned} \int_{-\infty}^{z} [(\chi * \varphi)(y) - \varphi(y)]\mathrm{d}y &= \int_{-\infty}^{z}\left[\int_{-\infty}^{+\infty} \chi(s)\varphi(y-s)\mathrm{d}s - \varphi(y)\right]\mathrm{d}y, \\ &= \int_{-\infty}^{z}\int_{-\infty}^{+\infty} \chi(s)[\varphi(y-s) - \varphi(y)]\mathrm{d}s\mathrm{d}y. \end{aligned}$$

By the same techniques as in the proof of (i), we have

$$\int_{-\infty}^{z}[(\chi*\varphi)(y)-\varphi(y)]\mathrm{d}y=-\int_{-\infty}^{+\infty}s\chi(s)\int_0^1\left[\int_{-\infty}^{z}\varphi'(y-\eta s)\mathrm{d}y\right]\mathrm{d}\eta\mathrm{d}s.$$

Then, we obtain

$$\int_{-\infty}^{z}[(\chi*\varphi)(y)-\varphi(y)]\mathrm{d}y=-\int_{-\infty}^{+\infty}s\ \chi(s)\int_0^1\varphi(z-\eta s)\mathrm{d}\eta\mathrm{d}s. \tag{51}$$

We have proved

$$\int_{-\infty}^{z}|(\chi*\varphi)(y)-\varphi(y)|\mathrm{d}y<+\infty.$$

□

Now, we establish the asymptotic behavior of the profile $\phi(z)$ when $z\to-\infty$.

Proposition 7. *Let ϕ be a traveling wave front of (27) connecting 0 to the positive equilibrium $N^\star$, with a speed $c>0$. Then, there exists a positive constant $\mu_0<\lambda^+(c)$ such that $\phi(z)=O(e^{\mu_0 z})$ as $z\to-\infty$. Moreover,*

$$\sup_{z\in\mathbb{R}}\left[e^{-\mu_0 z}\phi(z)\right]<+\infty. \tag{52}$$

Proof. We use Lemma 6 and the inequality (50). Then, for $y<\overline{y}_\varepsilon$

$$0\le J_\varepsilon\varphi(y)\le c\phi(y)-d_1\phi'(y)-\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)[(\chi*\varphi)(y)-\varphi(y)]. \tag{53}$$

By integrating the both sides of (53), from $-\infty$ to $z\le\overline{y}_\varepsilon$, we obtain

$$J_\varepsilon\int_{-\infty}^{z}\varphi(y)\mathrm{d}y\le c\varphi(z)-d_1\phi(z)-\frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)\int_{-\infty}^{z}[(\chi*\varphi)(y)-\varphi(y)]\mathrm{d}y.$$

Thanks to (51), we have

$$-\int_{-\infty}^{z}[(\chi*\varphi)(y)-\varphi(y)]\mathrm{d}y=\int_{-\infty}^{+\infty}s\chi(s)\int_0^1\varphi(z-\eta s)\mathrm{d}\eta\mathrm{d}s.$$

Since the function $\eta\in[0,1]\mapsto s\varphi(z-\eta s)$ is decreasing, we obtain

$$-\int_{-\infty}^{z}[(\chi*\varphi)(y)-\varphi(y)]\mathrm{d}y\le\left(\int_{-\infty}^{+\infty}s\chi(s)\mathrm{d}s\right)\varphi(z).$$

Then,

$$J_\varepsilon \int_{-\infty}^{z} \varphi(y)\mathrm{d}y \le c\varphi(z) - d_1\phi(z) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)\left(\int_{-\infty}^{+\infty} s\chi(s)\mathrm{d}s\right)\varphi(z).$$

We denote by

$$\begin{aligned} L_\varepsilon &= \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)\left(\int_{-\infty}^{+\infty} s\chi(s)\mathrm{d}s\right), \\ &= \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}(\beta_0-\varepsilon)cr\sum_{n=0}^{+\infty}(n+1)(2Ke^{-\gamma r})^n, \\ &= \frac{2(1-K)e^{-\gamma r}}{(1-2Ke^{-\gamma r})^3}(\beta_0-\varepsilon)cr. \end{aligned}$$

Hence, for all $z \le \overline{y}_\varepsilon$,

$$J_\varepsilon \int_{-\infty}^{z} \varphi(y)\mathrm{d}y + d_1\phi(z) \le (c+L_\varepsilon)\varphi(z). \tag{54}$$

This implies that, for all $z \le \overline{y}_\varepsilon$,

$$J_\varepsilon \int_{-\infty}^{0} \varphi(z+y)\mathrm{d}y \le (c+L_\varepsilon)\varphi(z).$$

Then, for all $z \le \overline{y}_\varepsilon$ and all $\eta > 0$, we have

$$J_\varepsilon \int_{-\eta}^{0} \varphi(z+y)\mathrm{d}y \le (c+L_\varepsilon)\varphi(z).$$

By integration by parts, we get for all $z \le \overline{y}_\varepsilon$ and all $\eta > 0$,

$$J_\varepsilon \eta\varphi(z-\eta) \le J_\varepsilon\left[\eta\varphi(z-\eta) + \int_0^{\eta} y\phi(z-y)\mathrm{d}y\right] \le (c+L_\varepsilon)\varphi(z).$$

We choose $\eta_0 > 0$ large enough such that

$$\theta_0 := \frac{c+L_\varepsilon}{J_\varepsilon \eta_0} \in (0,1).$$

Then, for all $z \le \overline{y}_\varepsilon$,

$$\varphi(z-\eta_0) \le \theta_0\varphi(z).$$

We put

$$j(x) = e^{-\mu_0 x}\varphi(x), \quad \text{for } x \in \mathbb{R},$$

with

$$\mu_0 = \frac{1}{\eta_0} \ln\left(\frac{1}{\theta_0}\right) = \frac{1}{\eta_0} \ln\left(\frac{J_\varepsilon \eta_0}{c + L_\varepsilon}\right).$$

We know that

$$\lim_{\eta_0 \to +\infty} \frac{1}{\eta_0} \ln\left(\frac{J_\varepsilon \eta_0}{c + L_\varepsilon}\right) = 0.$$

Then, we can choose $\eta_0 > 0$ large enough such that $\mu_0 < \lambda^+(c)$. On the one hand, we have $\varphi(x) = \int_{-\infty}^{x} \phi(y)\mathrm{d}y \leq \int_{-\infty}^{0} \phi(y)\mathrm{d}y + N^\star x$, for $x \geq 0$. Then, $\lim\limits_{x \to +\infty} j(x) = 0$. On the other hand, we have for $z \leq \overline{y}_\varepsilon$

$$j(z - \eta_0) = e^{-\mu_0(z-\eta_0)}\varphi(z - \eta_0) \leq \theta_0 e^{\mu_0 \eta_0} e^{-\mu_0 z}\varphi(z).$$

Recall that $\theta_0 e^{\mu_0 \eta_0} = 1$. Then, $j(z - \eta_0) \leq j(z)$, for all $z \leq \overline{y}_\varepsilon$. Consequently, there exists $j_0 > 0$ such that

$$j(z) \leq j_0, \quad \text{for all } z \in \mathbb{R}.$$

Thus,

$$\varphi(z) \leq j_0 e^{\mu_0 z}, \quad \text{for all } z \in \mathbb{R}.$$

Thanks to (54), we have $\phi(z) \leq \dfrac{c + L_\varepsilon}{d_1}\varphi(z)$. Then, we conclude that there exists $q_0 > 0$ such that

$$\phi(z) \leq q_0 e^{\mu_0 z}, \quad \text{for all } z \in \mathbb{R}.$$

This means that $\phi(z) = O(e^{\mu_0 z})$ as $z \to -\infty$. Moreover, since $z \mapsto \phi(z)$ and $z \mapsto e^{-\mu_0 z}$ are bounded on $(0, +\infty)$, we obtain

$$\sup_{z \in \mathbb{R}} \left[e^{-\mu_0 z}\phi(z)\right] < +\infty.$$

□

Remark 4. *Proposition 7 implies that the Laplace transform* $\displaystyle\int_{-\infty}^{+\infty} e^{-\lambda z}\phi(z)\mathrm{d}z$ *is well defined for all* $\lambda \in \mathbb{C}$ *such that* $0 < Re(\lambda) < \mu_0$.

Now, we study the non-existence of traveling front of (27).

Theorem 5. *Assume that* (1), (2), (17), (31), (35) *and* (45) *are satisfied. Moreover, assume that the functions* β *and* δ *are twice continuously differentiable on* $[0, N^\star]$. *Let* $c \in (0, c^\star)$. *Then, there is no traveling front of* (27).

Proof. We proof this theorem by contradiction. Let $c \in (0, c^\star)$ and assume that there exists a $\phi \in \Gamma$ such that

$$c\phi'(z) = d_1\phi''(z) - f(\phi(z)) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left(\chi * g(\phi)\right)(z). \tag{55}$$

Remark 4 implies that, for all $\lambda \in \mathbb{C}$ with $0 < Re(\lambda) < \mu_0$, the Laplace transform

$$\mathcal{L}(\lambda)(\phi) = \int_{-\infty}^{+\infty} e^{-\lambda z}\phi(z)\mathrm{d}z,$$

is well defined. Since $\phi \geq 0$, we know from [40] (Theorem 5b, page 58) that $\lambda \mapsto \mathcal{L}(\lambda)(\phi)$ is analytic for $0 < Re(\lambda) < \nu$ where ν is a real singularity of $\lambda \mapsto \mathcal{L}(\lambda)(\phi)$. We rewrite (55) in the following form

$$\begin{aligned} &- c\phi'(z) + d_1\phi''(z) - (\delta(0)+\beta(0))\phi(z) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta(0)\left(\chi * \phi\right)(z) = \\ &\quad - (\delta(0)+\beta(0))\phi(z) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta(0)\left(\chi * \phi\right)(z) + f(\phi(z)) \\ &\qquad - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\phi)\right)(z). \end{aligned} \tag{56}$$

Let $\lambda \in \mathbb{C}$ such that $0 < Re(\lambda) < \mu_0 < \lambda^+(c)$. The Fubini's theorem implies the following identity

$$\begin{aligned} \int_{-\infty}^{+\infty} e^{-\lambda z}(\chi * \phi)(z)\mathrm{d}z &= \int_{-\infty}^{+\infty} e^{-\lambda z}\int_{-\infty}^{+\infty}\chi(z-y)\phi(y)\mathrm{d}y\mathrm{d}z, \\ &= \int_{-\infty}^{+\infty}\phi(y)\int_{-\infty}^{+\infty} e^{-\lambda z}\chi(z-y)\mathrm{d}z\mathrm{d}y, \\ &= \int_{-\infty}^{+\infty}\phi(y)(\chi * e^{\lambda \cdot})(-y)\mathrm{d}y. \end{aligned}$$

The expression (29) leads to

$$\int_{-\infty}^{+\infty} e^{-\lambda z}(\chi * \phi)(z)\mathrm{d}z = \frac{(1-2Ke^{-\gamma r})e^{d_2 r\lambda^2 - cr\lambda}}{1-2Ke^{-\gamma r}e^{d_2 r\lambda^2 - cr\lambda}}\mathcal{L}(\lambda)(\phi).$$

By applying the Laplace transform to (56), we obtain

$$\begin{aligned} -\Delta_c(\lambda)\mathcal{L}(\lambda)(\phi) = \int_{-\infty}^{+\infty} e^{-\lambda z}\Big[f(\phi(z)) - (\delta(0)+\beta(0))\phi(z) \\ + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\beta(0)\left(\chi * \phi\right)(z) - \left(\chi * g(\phi)\right)(z)\right)\Big]\mathrm{d}z. \end{aligned} \tag{57}$$

Since $\lambda \mapsto \Delta_c(\lambda)$ and $\lambda \mapsto \mathcal{L}(\lambda)(\phi)$ are well defined for $0 < Re(\lambda) < \mu_0 < \lambda^+(c)$, then the right hand side of (57) is also well defined for $0 < Re(\lambda) < \mu_0$. Recall that $f(\phi(z)) = (\delta(\phi(z)) + \beta(\phi(z)))\phi(z)$ and $g(\phi)(z) = \beta(\phi(z))\phi(z)$, with $\beta,\ \delta \in C^2([0, N^\star])$. Moreover, $\lim_{z\to-\infty} \phi(z) = 0$. Then, Taylor's formula implies, that there exists $M > 0$ such that, when $z \to -\infty$,

$$0 \le f(\phi(z)) - (\delta(0) + \beta(0))\phi(z) \le M\phi^2(z) \text{ and } 0 \le \beta(0)\phi(z) - g(\phi)(z) \le M\phi^2(z).$$

Then,

$$0 \le \beta(0) \left(\chi * \phi\right)(z) - \left(\chi * g(\phi)\right)(z) = \left(\chi * [\beta(0)\phi - g(\phi)]\right)(z) \le M(\chi * \phi^2)(z).$$

So, there exits a positive constant (that we will call M) such that, when $z \to -\infty$

$$\begin{aligned} 0 \le f(\phi(z)) - (\delta(0)+\beta(0))\phi(z) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left[\beta(0) \left(\chi * \phi\right)(z) - \left(\chi * g(\phi)\right)(z)\right] \\ \le M \left[\phi^2(z) + (\chi * \phi^2)(z)\right]. \end{aligned}$$

Since $\phi(z) = O(e^{\mu_0 z})$ as $z \to -\infty$, and thanks to formula (29), we have the existence of a positive constant (that we will also call M) such that,

$$\phi^2(z) \le Me^{2\mu_0 z} \quad \text{and} \quad (\chi * \phi^2)(z) \le Me^{2\mu_0 z} \quad \text{as } z \to -\infty.$$

We have proved that

$$\begin{aligned} \int_{-\infty}^{+\infty} e^{-\lambda z} \Bigg[f(\phi(z)) - (\delta(0) + \beta(0))\phi(z) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \beta(0) \left(\chi * \phi\right)(z) \\ - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}} \left(\chi * g(\phi)\right)(z) \Bigg] \mathrm{d}z \end{aligned}$$

is well defined for all $\lambda \in \mathbb{C}$ with $0 < Re(\lambda) < 2\mu_0$. This means that $\lambda \mapsto \Delta_c(\lambda)\mathcal{L}(\lambda)(\phi)$ is well defined for $0 < Re(\lambda) < \min\{2\mu_0, \lambda^+(c)\}$, with $\lambda \mapsto \Delta_c(\lambda)$ well defined for $0 < Re(\lambda) < \lambda^+(c)$. Suppose that $2\mu_0 < \lambda^+(c)$. The fact that the integral $\mathcal{L}(\lambda)(\phi) := \int_{-\infty}^{+\infty} e^{-\lambda z}\phi(z)\mathrm{d}z$ is well defined for $0 < Re(\lambda) < 2\mu_0$, implies (see for instance [40], page 39) that $\phi(z) = O(e^{2\mu_0 z})$ as $z \to -\infty$. We can repeat this argument to prove that $\lambda \mapsto \mathcal{L}(\lambda)(\phi)$ is well defined for $0 < Re(\lambda) < \lambda^+(c)$. Now, we can say that all the expressions in (57) are defined for $0 < Re(\lambda) < \lambda^+(c)$. Furthermore, we have $\lim_{\lambda\to\lambda^+(c)} \Delta_c(\lambda) = -\infty$. Then, there exists $A > 0$ such that, for $\lambda \in \mathbb{R}$ with $A < \lambda < \lambda^+(c)$, we have

$$\Delta_c(\lambda)\phi(z) + f(\phi(z)) - (\delta(0) + \beta(0))\phi(z) + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\beta(0)\left(\chi * \phi\right)(z) \\ - \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\chi * g(\phi)\right)(z) < 0.$$

If we multiply this inequality by $e^{-\lambda z}$ and integrate it, we obtain

$$\int_{-\infty}^{+\infty} e^{-\lambda z}\Big[\Delta_c(\lambda)\phi(z) + f(\phi(z)) - (\delta(0) + \beta(0))\phi(z) \\ + \frac{2(1-K)e^{-\gamma r}}{1-2Ke^{-\gamma r}}\left(\beta(0)\left(\chi * \phi\right)(z) - \left(\chi * g(\phi)\right)(z)\right)\Big]\,\mathrm{d}z < 0.$$

This last inequality is in contradiction with (57). The conclusion is that (27) has no front connecting 0 and the positive equilibrium $N^\star$. □

6. Numerical simulations and discussion

We can numerically solve the system (8) to show the existence and attractivity of traveling waves. Let us take

(i) $\beta(N) = \dfrac{\beta_0\theta^\alpha}{\theta^\alpha + N^\alpha}$, $\alpha > 1$,
(ii) $\delta(N) = \hat{\delta}N^\kappa$, $\hat{\delta} > 0$ and $\kappa \geq 1$.

It is clear that, for such a choice, the assumptions (1), (2) and (19) are always satisfied. Assume that the condition (17) is satisfied. That is

$$2Ke^{-\gamma r} < 1.$$

The function $h : N \in [0, +\infty) \mapsto h(N) = \dfrac{\delta(N)}{\beta(N)}$ is given by

$$h(N) = \frac{\hat{\delta}}{\beta_0\theta^\alpha}N^\kappa\left(\theta^\alpha + N^\alpha\right).$$

Obviously, h is increasing on $[0, +\infty)$ and satisfies $h(0) = 0$ and $\lim\limits_{N\to+\infty} h(N) = +\infty$. Furthermore, suppose that $2e^{-\gamma r} > 1$. Then, there exists a unique $N^\star > 0$ such that

$$h(N^\star) = \frac{2e^{-\gamma r} - 1}{1 - 2Ke^{-\gamma r}}.$$

For simplicity we take $\kappa = \alpha > 1$. It is clear that the function $N \mapsto \beta(N)N$ is increasing on the interval $\left[0, \theta/(\alpha-1)^{1/\alpha}\right]$. Then, it suffices to check that $N^\star \le \theta/(\alpha-1)^{1/\alpha}$. We have

$$h\left(\frac{\theta}{(\alpha-1)^{1/\alpha}}\right) = \frac{\alpha}{(\alpha-1)^2}\frac{\hat{\delta}\theta^\alpha}{\beta_0}.$$

Then, $N^\star \le \theta/(\alpha-1)^{1/\alpha}$ if and only if

$$\frac{\hat{\delta}\theta^\alpha}{\beta_0} \ge \frac{(\alpha-1)^2}{\alpha} \times \frac{2e^{-\gamma r}-1}{1-2Ke^{-\gamma r}}.$$

It is easy to see that (45) is equivalent to $\beta'(0) + \delta'(0) > 0$. It is also equivalent to $\theta^\alpha \ge \beta_0/\hat{\delta}$. We conclude that a necessary and sufficient condition to have (31) and (45) is the following

$$\frac{\hat{\delta}\theta^\alpha}{\beta_0} \ge \max\left\{1, \frac{(\alpha-1)^2}{\alpha} \times \frac{2e^{-\gamma r}-1}{1-2Ke^{-\gamma r}}\right\}.$$

We summarize these results in the following corollary.

Corollary 3. *Suppose that the following hypotheses hold.*

(i) $N \mapsto \beta(N) = \dfrac{\beta_0\theta^\alpha}{\theta^\alpha + N^\alpha}$, $N \mapsto \delta(N) = \hat{\delta}N^\alpha$, $\hat{\delta} > 0$ *and* $\alpha > 1$,

(ii) $\dfrac{1}{\gamma}\ln(2K) < r < \dfrac{1}{\gamma}\ln(2)$,

(iii) $\dfrac{\hat{\delta}\theta^\alpha}{\beta_0} \ge \max\left\{1, \dfrac{(\alpha-1)^2}{\alpha} \times \dfrac{2e^{-\gamma r}-1}{1-2Ke^{-\gamma r}}\right\}$.

Then, (1), (2), (17), (19), (31), (35) *and* (45) *are satisfied.*

We have examined the traveling wave fronts for a new type of delay differential system which is formed by a reaction-diffusion equation and a difference equation with delay. By the method of upper and lower solutions, we have proved the existence of traveling wave fronts. An upper solution gives rise to a traveling wave as limit of monotone iterations and a lower solution allows us to connect the trivial equilibrium to the positive uniform one. We have proved that there is a minimal wave speed $c^\star > 0$ by using a characteristic equation. The result on the existence of traveling waves in Theorem 3 is valid not only for $c > c^\star$ but also for $c = c^\star$ (Theorem 4). Furthermore, Proposition 7 shows that all traveling waves of system (8) with speed $c > c^\star$ and $c = c^\star$ possess the prior asymptotic behavior (52).

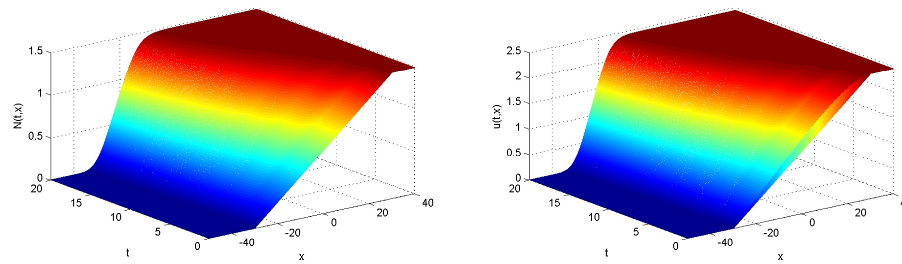

Figure 3: The numerical solution of $N(t,x)$ and $u(t,x)$. Parameters are: $\gamma = 0.2$ day^{-1}, $r = 2.5$ days, $\beta_0 = 1.77$ day^{-1}, $\delta = 0.05$ day^{-1}, $\alpha = 3$ day^{-1}, $d_1 = 5$ day^{-1}, $d_2 = 1$ day^{-1} and $\theta = 3$ cell.g^{-1}.

In Figure 3, we numerically illustrated the solutions $(N(t,x), u(t,x))$ of system (8). It is seen that the obtained solutions converge to a traveling front propagating without the change of the profile.

Concerning the study of asymptotic speeds of spread, as we mentioned in the introduction the techniques worked out in [17, 22, 35] cannot be applied to the system (8). However, a partial result can be proved by a direct method.

Proposition 8. *Assume that* (1) *and* (45) *hold true. Let* (N,u) *be a solution of* (8)*. If the initial condition* (N_0, u_0) *is null for* x *outside a compact set, then*

$$\lim_{t\to+\infty,\, |x|\geq ct} (N,u) = (0,0) \quad \textit{for } c > c^\star.$$

Proof. The idea of the proof is adapted from [45]. Let $c > 0$. We choose $0 < \lambda < \lambda^+(c)$ such that $\Delta_c(\lambda) > 0$. We put $\overline{N}(t,x) = Me^{\lambda(ct-zx)}$ and $\overline{u}(t,x) = M\beta_0 e^{\lambda(ct-zx)}/(1-2Ke^{-\gamma r}e^{d_2 r\lambda^2 - cr\lambda})$, for some $M > 0$ and $z = \pm 1$. Using the lemma 2, we have

$$\overline{u}(t,x) = \beta_0 \overline{N}(t,x) + 2Ke^{-\gamma r} \int_{-\infty}^{+\infty} \Gamma_2(r, x-y)\overline{u}(t-r,y)dy.$$

On the other hand, we have

$$\begin{aligned} &\frac{\partial \overline{N}(t,x)}{\partial t} - d_1 \frac{\partial^2 \overline{N}(t,x)}{\partial x^2} + (\delta_0 + \beta_0)\overline{N}(t,x) \\ &\qquad\qquad -2(1-K)e^{-\gamma r} \textstyle\int_{-\infty}^{+\infty} \Gamma_2(r, x-y)\overline{u}(t-r,y)dy \\ &= \overline{N}(t,x)\Delta_c(\lambda) > 0. \end{aligned}$$

So, $(\overline{N}, \overline{u})$ is an upper solution of the linear system

$$\begin{cases} \dfrac{\partial N(t,x)}{\partial t} = d_1 \dfrac{\partial^2 N(t,x)}{\partial x^2} - (\delta_0 + \beta_0) N(t,x) \\ \qquad\qquad\qquad +2(1-K)e^{-\gamma r} \int_{-\infty}^{+\infty} \Gamma_2(r, x-y) u(t-r, y) dy, \\ u(t,x) = \beta_0 N(t,x) + 2K e^{-\gamma r} \int_{-\infty}^{+\infty} \Gamma_2(r, x-y) u(t-r, y) dy. \end{cases} \tag{58}$$

Let $c > c^\star$ and we fix $\tilde{c} \in (c^\star, c)$. From Lemma 4, we ensure that there exists $0 < \tilde{\lambda} < \lambda^+(c)$ such that $\Delta_{\tilde{c}}(\tilde{\lambda}) > 0$. Using the fact that (N_0, u_0) has a compact support, we can choose M large enough such that, for $z = \pm 1$ and $(\theta, x) \in [-r, 0] \times \mathbb{R}$,

$$N_0(x) \leq M e^{-\tilde{\lambda} z x} \quad \text{and} \quad u_0(\theta, x) \leq \frac{M \beta_0 e^{\tilde{\lambda}(\tilde{c}\theta - zx)}}{1 - 2K e^{-\gamma r} e^{d_2 r \tilde{\lambda}^2 - \tilde{c} r \tilde{\lambda}}}.$$

Furthermore, the solution (N, u) of the system (8) satisfies

$$\begin{cases} \dfrac{\partial N(t,x)}{\partial t} \leq d_1 \dfrac{\partial^2 N(t,x)}{\partial x^2} - (\delta_0 + \beta_0) N(t,x) \\ \qquad\qquad\qquad +2(1-K)e^{-\gamma r} \int_{-\infty}^{+\infty} \Gamma_2(r, x-y) u(t-r, y) dy, \\ u(t,x) \leq \beta_0 N(t,x) + 2K e^{-\gamma r} \int_{-\infty}^{+\infty} \Gamma_2(r, x-y) u(t-r, y) dy. \end{cases}$$

Then, (N, u) is a lower solution of (58). By the comparison principle, we have, for all $(t, x) \in [0, +\infty) \times \mathbb{R}$,

$$N(t,x) \leq M e^{\tilde{\lambda}(\tilde{c}t - zx)} \quad \text{and} \quad u(t,x) \leq \frac{M \beta_0 e^{\tilde{\lambda}(\tilde{c}t - zx)}}{1 - 2K e^{-\gamma r} e^{d_2 r \tilde{\lambda}^2 - \tilde{c} r \tilde{\lambda}}}.$$

We put, for $x \neq 0$, $z = x/|x|$ and we get

$$N(t,x) \leq M e^{\tilde{\lambda}(\tilde{c}t - |x|)} \quad \text{and} \quad u(t,x) \leq \frac{M \beta_0 e^{\tilde{\lambda}(\tilde{c}t - |x|)}}{1 - 2K e^{-\gamma r} e^{d_2 r \tilde{\lambda}^2 - \tilde{c} r \tilde{\lambda}}}.$$

This proves the result. $\square$

The existence of the limit

$$\lim_{t \to +\infty, \, |x| \leq ct} (N, u), \quad \text{for } 0 < c < c^\star,$$

and the asymptotic stability of traveling waves of (8) seem to be a challenging problem and probably need the development of new techniques. We leave this study for a future work.

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