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SPATIAL DYNAMICS FOR A NON-MONOTONE REACTION-DIFFUSION SYSTEM WITH SPATIO-TEMPORAL DELAY

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Abstract. In this paper, we study the spreading speed and traveling wave solutions of a non-monotone reaction-diffusion system with spatio-temporal delay. By constructing a pair of auxiliary systems and using the Schauder 's fixed point theorem, the existence of the spreading speed is proved, which is consistent with the minimum wave speed of the traveling wave solution. The results show that the spreading speed and the traveling wave solution are convergent upward.

1. Introduction

Reaction-diffusion systems can be used to describe the dynamic behavior of many mathematical models, such as disease transmission, population diffusion and biological invasion [20]. A classical reaction-diffusion equation is

$$U_t = DU_{xx} + F(U(x,t)), \tag{1.1}$$

where $(x,t) \in \mathbb{R} \times [0,+\infty)$ and $D > 0$ is the diffusion coefficient. The traveling wave solution $\phi(x+ct)$ represents a special class of solutions invariant under spatial translation, with c denoting the wave speed. Closely related is the notion of spreading speed, first introduced by Aronson and Weinberger [1], which describes the asymptotic rate at which the leading edge of an initially localized population advances into unoccupied space. In population dynamics, it quantifies the range expansion driven by the interplay between local growth and spatial dispersal. Mathematically, the spreading speed corresponds to the minimal wave speed of traveling fronts or the asymptotic propagation speed of population level sets.

In natural plant communities, many species rely on the formation of a *seed bank* to buffer environmental fluctuations and resist external disturbances, thereby enhancing long-term population persistence. Dormant individuals, typically in the form of seeds stored in the soil, do not participate in immediate ecological processes but can germinate and return to the active population when conditions become favorable. This dormancy–activation mechanism plays a vital ecological role in maintaining multi-generational continuity, avoiding short-term extinction, and enhancing ecosystem resilience. To investigate the spatiotemporal dynamics associated with the seed bank mechanism, we consider a local reaction-diffusion model, which was presented by Hadeler and Lewis [13],

$$\begin{cases} U_t = DU_{xx} + F(U(x,t)) - \gamma_1 U(x,t) + \gamma_2 V(x,t), \\ V_t = \gamma_1 U(x,t) - \gamma_2 V(x,t), \end{cases} \tag{1.2}$$

where $U(x,t)$ denotes the density of *active individuals* (e.g., growing plants) at position x and time t, while $V(x,t)$ represents the density of *dormant seeds* in the seed bank. Active individuals can diffuse

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through space with diffusion coefficient D, and their local growth is governed by a nonlinear function $F(U)$. The parameters γ_1 and γ_2 represent the transition rates from active to dormant states and vice versa, respectively. The asymptotic behavior of system (1) in both unbounded and bounded domains was first investigated by Zhang and Zhao [34]. Subsequently, Zhang and Li [35] proved the monotonicity and uniqueness of traveling wave solutions for the same system.

To further capture *time delays* inherent in plant life cycles, such as seed germination lag or delayed environmental responses, model (1) is extended to the following delay reaction-diffusion system[15, 23]:

$$\begin{cases} U_t = DU_{xx} + F(U(x,t), V(x,t-\tau)) - \gamma_1 U(x,t) + \gamma_2 V(x,t), \\ V_t = \gamma_1 U(x,t) - \gamma_2 V(x,t). \end{cases} \tag{1.3}$$

In system (1.3), the growth function F depends on the current density of active individuals U and the delayed density of dormant individuals V evaluated at $t-\tau$, thereby incorporating physiological lags associated with activation, germination, and reproduction. The inclusion of this delay term provides a more faithful representation of the temporal influence exerted by the seed bank on active population dynamics. Wu and Zhao [29] established the existence of the minimal wave speed, monotonicity and uniqueness (up to translation) of the traveling wave fronts under the assumption that $F(U,V)$ is monotone with respect to V. By using comparison arguments, Schauder's fixed-point theorem and a limiting process, Zhao and Liu [37] obtained the spreading speed and its coincidence with the minimal wave speed of traveling wave solutions of system (1.3) in non-quasi-monotone case. Using the weighted-energy method and comparison principle, Zhou et al. [36] discussed the stability of traveling wavefronts for a spatially nonlocal population model with quasi-monotonicity and delay of the system (1.3), it was shown that all monostable wavefronts were exponentially stable for large speeds.

In certain situations, incorporating only a discrete delay or a finite delay into a population model proves to be insufficient. Britton [4, 5] first introduced the notion of a nonlocal delay, which has since stimulated extensive research on the spatial dynamics of reaction-diffusion systems with nonlocal delays [2, 6, 7, 9, 18, 20, 21, 22, 26, 27, 28, 30]. Recently, Bai and Zhao [3] considered the following model:

$$\begin{cases} U_t = DU_{xx} + F\left(U(x,t), \int_{\mathbb{R}} G(y)B(U(x-y,t-\tau))dy\right) - \gamma_1 U(x,t) + \gamma_2 V(x,t), \\ V_t = \gamma_1 U(x,t) - \gamma_2 V(x,t), \end{cases} \tag{1.4}$$

they studied the spreading speed and traveling wave solutions of system (1.4) without quasi-monotonicity. For a detailed discussion of the spatial dynamics of the nonlocal diffusion version of model , please refer to [17, 39].

Motivated by the above, we consider the following reaction-diffusion equations with spatio-temporal delay,

$$\begin{cases} U_t = DU_{xx} + F\left(U(x,t), \left(G**B(U)\right)(x,t)\right) - \gamma_1 U(x,t) + \gamma_2 V(x,t), \\ V_t = \gamma_1 U(x,t) - \gamma_2 V(x,t), \end{cases} \tag{1.5}$$

where $x \in \mathbb{R},\ t \geq 0$, and the convolution term is defined by

$$(G**B(U))(x,t) = \int_0^{+\infty} \int_{\mathbb{R}} G(y,s)B(U(x-y,t-s))\,dy\,ds,$$

which represents the cumulative influence of previously existing individuals at past times $t-s$ and spatial positions $x-y$ on the current dynamics at (x,t). The kernel function $G(y,s)$ describes the spatial and temporal weighting of these influences, while $B(U)$ captures the biological contribution (e.g., fecundity) of active individuals. Note that, when $G(x,t) = \delta(x)\delta(t-\tau)$ (where $\delta(\cdot)$ is the Dirac delta function), (1.5) degenerates to (1.3). When $G(x,t) = k(x)\delta(t-\tau)$, (1.5) degenerates to (1.4). Hence, model (1.5) is applicable in a broader context, making it more general.

The purpose of this paper is to study the spreading speed and traveling wave solutions of (1.5) without quasi-monotonicity. In particular, we investigate the effect of spatio-temporal delay on the propagation speed and traveling wave solutions. Two auxiliary quasi-monotone systems are introduced, and a comparison principle is established between the Cauchy problems of the original system and the auxiliary systems. The proof method of this paper is inspired by [3, 37], but the analysis is much more complicated. In particular, the primary difficulty lies in the coupling of time-delay terms with spatial variables, which yields a particularly intricate integrand. The following is the assumptions:

(A1) $G(-y,s) = G(y,s) \geq 0$ for $y \in \mathbb{R}$ and $s \geq 0$, $G**1 = 1$, that is to say,

$$\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)\,dy\,ds = 1;$$

in addition, there is a positive real number $\lambda_0 \in (0,+\infty)$ such that when $\lambda \in [0,\lambda_0)$ (here λ_0 may be $+\infty$), for any wave speed $c > 0$, there holds

$$\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\lambda(y+cs)}\,dy\,ds < +\infty.$$

(A2) $F(\cdot) \in C^2(\mathbb{R}_+^2,\mathbb{R})$ and $B(\cdot) \in C^2(\mathbb{R}_+,\mathbb{R}_+)$ have $\partial_1 F(0,0) < 0$, with $B(0) = 0$ and $B(U) > 0$ for $U > 0$, $F(0,B(0)) = F(K,B(K)) = 0$ and $F(U,B(U)) > 0$ for $U \in (0,K)$, $F(U,B(U)) < 0$ for $U > K$.

(A3) $F(\cdot)$ and $B(\cdot)$ are strictly subhomogeneous, that is $F(\delta U,\delta V) > \delta F(U,V)$ and $B(\delta U,\delta V) > \delta B(U,V)$ for any $\delta \in (0,1), U,V > 0$.

(A4) There exist $K^\pm$ and K with $0 < K^- \leq K \leq K^+$ and twice piecewise consitinuously differentiable functions $B^\pm : [0,K^+] \to \mathbb{R}_+$ and $F^\pm : \bar{I} \to \mathbb{R}$ such that
  (i) $F^\pm(0,B^\pm(0)) = 0, F^\pm(K^\pm,B^\pm(K^\pm)) = 0, (B^\pm)'(0) = B'(0)$ and $\partial_i F^\pm(0,0) = \partial_i F(0,0), i = 1,2$ and $\partial_1 F^\pm \in C(\bar{I},\mathbb{R})$.
  (ii) $B^\pm(U)$ are non-decreasing on $[0,K^\pm]$, $B^\pm(0) = 0$ and $0 < B^-(U) \leq B(U) \leq B^+(U)$for $U \in (0,K^+]$. $F^\pm(U,V)$ are non-decreasing with respect to V on $\bar{I}$ and $F^-(U,V) \leq F(U,V) \leq F^+(U,V),\ \forall (U,V) \in \bar{I}$, so we also have $F^\pm(0,0) = F(0,0) = 0$.
  (iii) $F^\pm(\cdot)$ is strictly subhomogeneous on $\bar{I}$ and $B^\pm(\cdot)$ is strictly subhomogeneous on $[0,K^+]$. Together with (ii) of (A4) imply that for any $\delta \in (0,1)$,

$$F^\pm(\delta K^\pm, B^\pm(\delta K^\pm)) > \delta F^\pm\left(K^\pm, \frac{B^\pm(\delta K^\pm)}{\delta}\right) \geq \delta F^\pm(K^\pm,B^\pm(K^\pm)) = 0,$$

  so with $F^\pm(U,B^\pm(U)) > 0$ for $U \in (0,K^\pm)$, and hence there is no other positive zeros of $F^\pm$ on $[0,K^\pm] \times [0,S^\pm(K^\pm)]$.
  Here, and in what follows, we define $\bar{I} := [0,K^+] \times [0,B^+(K^+)]$.

Remark 1.1. In view of (A2)-(A4), it follows from [38, Lemma 2.3.2] that

$$0 < B(U) \leq B'(0)U,\ \forall\ U \in (0,K),$$
$$0 < F(U,B(U)) \leq \partial_1 F(0,0)U + \partial_2 F(0,0)B'(0)U,\ \forall\ U \in (0,K),$$

which imply that $B'(0) > 0$ and $\partial_1 F(0,0) + \partial_2 F(0,0)B'(0) > 0$.

The rest of this paper is organized as follows. In section 2, we present preliminaries. In section 3, the existence of the spreading speed c^* of system (1.5) in the non-monotonic case is proved by using the method of fluctuation and comparative argument. In section 4, we obtain the existence of traveling wave solutions($c \geq c^*$) by using the fixed point theorem and the method of limit argument. In section 5, we provide an ecological interpretation of the results.

2. Preliminaries

In this section, we study the spreading speed and traveling wave solutions of (1.5) in the quasi-monotone case. For this reason, we make the following assumptions:

(A5) $\partial_2 F(U,V) > 0$ for all $(U,V) \in [0,K] \times [0,B(K)]$ and $B(U)$ is non-decreasing on $[0,K]$.

Note that if (A5) holds, then we can replace $F^{\pm}(U,V), B^{\pm}(U), K^{\pm}$ with $F(U,V), B(U), K$. By assumption (A2), we can deduce that system (1.5) has two equilibrium points $\mathbf{0} := (0,0)$ and $\mathbf{K} := (K,\bar{K})$ with $K = (\gamma_2/\gamma_1)\bar{K}$. It follows from [3] that we get the following results.

2.1. **The spatially homogeneous system.** We start with the global dynamics of the following spatially homogeneous system:

$$\begin{cases} \frac{dU}{dt} = F(U(t), B(t-\tau))) - \gamma_1 U(t) + \gamma_2 V(t), \\ \frac{dV}{dt} = \gamma_1 U(t) - \gamma_2 V(t), \end{cases} \tag{2.1}$$

we define $N := C([-\tau,0],[0,K]\times[0,\bar{K}])$. Then we have the following result.

Lemma 2.1. [3] *Let (A2)-(A3) and (A5) hold. For any $\phi \in N$, system (2.1) has a unique solution $W(t,\phi)$ with $W_0 = \phi$, and $W_t(\phi) := (U_t(\phi), V(t,\phi)) \in N$ for all $t \geq 0$.*

Through [3, Lemma 2.1] and [12, Theorems 2.2.1 and 2.2.3] and [33, Theorem 3.2], we can get the conclusion that $\mathbf{K} = (K,\bar{K})$ is globally asymptotically stable for system (2.1) in $N \backslash \{\mathbf{0}\}$.

2.2. **Results for monotone delayed system.** Since system (1.5) is cooperative and its solution maps are monotone, we can use the general theory developed in [16] to study the spreading speeds for (1.5). We start with some basic notations.

Let $X := \mathrm{BUC}\left(\mathbb{R},\mathbb{R}^2\right)$ be the Banach space of all bounded and uniformly continuous functions from $\mathbb{R}$ into $\mathbb{R}^2$ with the usual supremum norm $\|\cdot\|_X$, and $X^+ := \{\phi \in X : \phi(x) \geq 0, \forall x \in \mathbb{R}\}$. The space $\mathrm{BUC}(\mathbb{R},\mathbb{R})$ is defined similarly. Clearly, any vector in $\mathbb{R}^2$ can be regarded as a function in X.

Let Y be the space of all continuous functions from $[-\tau,0]$ to $\mathbb{R}^2$ with the usual supremum norm $\|\cdot\|_Y$, i.e., $Y = C([-\tau,0],\mathbb{R}^2)$, and $Y_+ = C([-\tau,0],\mathbb{R}^2_+)$. Then (Y,Y_+) is an ordered Banach space. For $U,V \in Y$, we write $U \geq V$ if $U - V \in Y_+$, $U > V$ if $U - V \in Y_+ \backslash \{0\}$, and $U \gg V$ if $U - V \in \mathrm{Int}(Y_+)$. Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to Y equipped with the compact open topology, that is, $U_m \to U$ in $\mathcal{C}$ means that the sequence of $U_m(x)$ converges to $U(x)$ in Y as $m \to \infty$ uniformly for x in any compact subset of $\mathbb{R}$. For $U,V \in \mathcal{C}$, we write $U \geq V$ ($U \gg V$) provided $U(x) \geq V(x)$ ($U(x) > V(x)$), $\forall x \in \mathbb{R}$ and $U > V$ provided $U \geq V$ but $U \neq V$. Clearly, any element in Y can be regarded as a constant function in $\mathcal{C}$. Moreover, for each $r \in Y$ with $r \gg 0$, we define $Y_r := \{U \in Y : 0 \leq U \leq r\}$ and $\mathcal{C}_r := \{U \in \mathcal{C} : U(x) \in Y_r, \forall x \in \mathbb{R}\}$. As usual, we identify an element $\phi \in \mathcal{C}$ as a function from $\mathbb{R} \times [-\tau,0]$ into $\mathbb{R}^2$ by $\phi(x,\theta) = \phi(x)(\theta)$.

Define the reflection operator R by $R[U](x,\theta) = U(-x,\theta)$, and the translation operator T_y by $T_y[U](x,\theta) = U(x-y,\theta)$ for each $y \in \mathbb{R}$. Let $Q : \mathcal{C}_r \to \mathcal{C}_r$ be a given map. The following assumptions on map Q will be referred to:

(C1) $Q[R[U]] = R[Q[U]], T_y[Q[U]] = Q[T_y[U]], \forall U \in \mathcal{C}_r, y \in \mathbb{R}$.

(C2) $Q : \mathcal{C}_r \to \mathcal{C}_r$ is continuous with respect to the compact open topology.

(C3) $\{Q[U](x,\cdot) : U \in \mathcal{C}_r, x \in \mathbb{R}\}$ is precompact in Y.

(C4) Q is monotone (order preserving) in the sense that $Q[U] \geq Q[V]$ whenever $U \geqslant V$ in $\mathcal{C}_r$.

(C5) $Q : Y_r \to Y_r$ admits exactly two fixed points 0 and r and $\lim_{n\to\infty} Q^n[y] = r$ for any $y \in Y_r$ with $y \gg 0$.

Define a family of linear operators $T(t) = \mathrm{diag}\,(T_1(t), T_2(t))$ with $T(0) = I$ for $t \geq 0$ and

$$T_i(t)\phi(x) = \int_{\mathbb{R}} \Gamma_i(x-y,t)\phi(y)dy, \ \forall\ \phi \in \mathrm{BUC}(\mathbb{R},\mathbb{R}), t > 0,$$

where

$$\Gamma_1(x,t) = \frac{1}{\sqrt{4\pi Dt}} e^{-\frac{x^2}{4Dt}-\gamma_1 t}, \ \ \Gamma_2(x,t) = e^{-\gamma_2 t}\delta(x)$$

and $\delta(\cdot)$ is the Dirac function. Define $\Upsilon = (\Upsilon_1, \Upsilon_2) : \mathcal{C} \to X$ by

$$\Upsilon_1 (\phi_1, \phi_2)(x) := F\left(\phi_1(x,0), \int_0^{+\infty}\int_{\mathbb{R}} G(y,s)B(\phi_1(x-y,-s))\,dyds\right) + \gamma_2\phi_2(x,0), \ \forall\ x \in \mathbb{R},$$
$$\Upsilon_2 (\phi_1, \phi_2)(x) := \gamma_1\phi_1(x,0), \ \forall\ x \in \mathbb{R}.$$

For convenience, we express (1.5) as the following integral form

$$W(x,t) = T(t)W(\cdot,0)(x) + \int_0^t T(t-\hat{s})\Upsilon(W_{\hat{s}})(x)d\hat{s}, \ \forall\ (x,t) \in \mathbb{R}\times(0,\infty), \tag{2.2}$$

where $W(x,t) := (U(x,t), V(x,t))$.

By using the theory of abstract functional differential equations proposed in [19], we can establish the following conclusions :

Lemma 2.2. *Assume that (A1)-(A3) and (A5) hold. For any $\phi = (\phi_1, \phi_2) \in \mathcal{C}_{\mathbf{K}}$, the system (1.5) admits a unique solution $W(x,t;\phi) := (U(x,t;\phi), V(x,t;\phi))$ which exists globally in time $t \geq -\tau$ and satisfies the initial condition $W_0 = \phi$, moreover, it ensures that $W_t \in \mathcal{C}_{\mathbf{K}}$ for all $t \geq 0$, where $W_t(x,\theta;\phi) = W(x,t+\theta;\phi)$ for any $t > 0,\ x \in \mathbb{R},\ \theta \in [-\tau, 0]$,*

Now we let $W(x,t;\phi)$ be the solution of (1.5) with initial value $\phi \in \mathcal{C}_{\mathbf{K}}$. Define $Q_t : \mathcal{C}_{\mathbf{K}} \to \mathcal{C}_{\mathbf{K}}$ by

$$[Q_t(\phi)](x,\theta) = W_t(x,\theta;\phi), \ \forall\ t \geq 0, x \in \mathbb{R}, \theta \in [-\tau, 0].$$

It is easy to see that $Q_0 = I$, and $Q_{t+\hat{s}} = Q_t \circ Q_{\hat{s}}$ for all $t, \hat{s} \geqslant 0$. By arguments similar to those in [10, Lemma 4.3], we can show that $\{Q_t\}_{t\geq 0}$ is a monotone semiflow on $\mathcal{C}_{\mathbf{K}}$ with time-one map Q_1 satisfying (A1)-(A5). It then follows from [16, Theorems 2.11 and 2.15] that Q_1 admits a spreading speed $c^* > 0$. The following result shows that c^* is also the spreading speed of (4).

Theorem 2.3. *Assume (A1)-(A3) and (A5) hold. Then the following statements are valid:*

(i) For any $c > c^*$, if $\mathbf{0} \leq \phi \ll \mathbf{K}$ and $\phi(x,\cdot) = \mathbf{0}$ for x outside a bounded interval, then

$$\lim_{t\to\infty, |x|\geq ct} W(x,t;\phi) = \mathbf{0}.$$

(ii) For any $c \in (0, c^*)$, if $\phi := (\phi_1, \phi_2) \in \mathcal{C}_{\mathbf{K}}$ and either $\phi_1 \not\equiv 0$ or $\phi_2(\cdot, 0) \not\equiv 0$ holds, then

$$\lim_{t\to\infty, |x|\leq ct} W(x,t;\phi) = \mathbf{K}.$$

Proof. We use the similar arguments in the proof of [32, Theorem 4.1]. Statement(i) follows from [16, Theorem 2.17(i)]. To prove statement (ii), we first make the following proposition:

Proposition 2.4. *For any $\phi = (\phi_1, \phi_2) \in \mathcal{C}_{\mathbf{K}}$, if either $\phi_1 \not\equiv 0$ or $\phi_2(\cdot, 0) \not\equiv 0$, then $W(x,t;\phi) \gg 0$ for all $x \in \mathbb{R},\ t > \tau,$ and hence, $Q_t(\phi) \gg 0$ for $t > 2\tau$.*

If $\phi_1 \neq 0$, then there exists a number $\beta > 0$ and an interval $[a_1, a_2] \times [b_1, b_2] \subset \mathbb{R} \times [-\tau, 0]$ such that

$$\phi_1(x, \theta) \geq \beta, \ \forall\ (x, \theta) \in [a_1, a_2] \times [b_1, b_2].$$

By Lemma 2.2, $W(x, t; \phi) \geq \mathbf{0}$ for all $x \in \mathbb{R}$ and $t \geq 0$. Let $M = \max_{(U,V)\in[0,K]\times[o,B(K)]} |\partial_1 F(U, V)|$, then the first equation of (1.5) satisfies

$$\begin{aligned} U_t =& DU_{xx} + J_1(x,t)U(x,t) + J_2(x,t) - \gamma_1 U(x,t) + \gamma_2 V(x,t) \\ \geq& DU_{xx} + (J_1(x,t) - \gamma_1)U(x,t) + J_2(x,t) \\ \geq& DU_{xx} - (M + \gamma_1)U(x,t) + J_2(x,t), \end{aligned} \tag{2.3}$$

where

$$\begin{aligned} J_1(x,t) &= \int_0^1 \partial_1 F\left(\theta U(x,t), \theta \int_0^{+\infty}\int_{\mathbb{R}} G(y,s)B(U(x-y,t-s))dyds\right) d\theta, \\ J_2(x,t) &= \int_0^1 \partial_2 F\left(\theta U(x,t), \theta \int_0^{+\infty}\int_{\mathbb{R}} G(y,s)B(U(x-y,t-s))dyds\right) d\theta \\ &\quad \times \int_0^{+\infty}\int_{\mathbb{R}} G(y,s)B(U(x-y,t-s))dyds. \end{aligned}$$

By (2.2) and (2.3), we have

$$\begin{aligned} & U(x,\tau;\phi) \\ \geq& \int_{\mathbb{R}} \Gamma(x-y,\tau)\phi_1(y,0)dy + \int_0^\tau \int_{\mathbb{R}} \Gamma(x-y,\tau-\hat{s})J_1(y,\hat{s})dyd\hat{s} \\ \geq& \int_0^\tau \int_{\mathbb{R}} \Gamma(x-y,\tau-\hat{s}) \int_0^1 \Big[\partial_2 F(\theta U(y,\hat{s}), \theta \int_0^{+\infty}\int_{\mathbb{R}} G(\xi,s)B(U(y-\xi,\hat{s}-s))d\xi ds) \\ & \times \int_0^{+\infty}\int_{\mathbb{R}} G(\xi,s)B(U(y-\xi,\hat{s}-s))d\xi ds\Big] d\theta dyd\hat{s} \\ \geq& \int_{-\tau}^0 \int_{\mathbb{R}} \Gamma(x-y,-\hat{s}') \int_0^1 \Big[\partial_2 F(\theta U(y,\tau+\hat{s}'), \theta \int_0^{+\infty}\int_{\mathbb{R}} G(\xi,s)B(U(y-\xi,\tau+\hat{s}'-s))d\xi ds) \\ & \times \int_0^{+\infty} G(\xi,s)B(U(y-\xi,\tau+\hat{s}'-s))d\xi ds\Big] d\theta dyd\hat{s}' \\ \geq& B(\beta)\int_{b_1}^{b_2}\int_{\mathbb{R}} \Gamma(x-y,-\hat{s}') \int_0^1 \Big[\partial_2 F(\theta U(y,\tau+\hat{s}'), \\ & \theta \int_0^{+\infty}\int_{\mathbb{R}} G(\xi,s)B(U(y-\xi,\tau+\hat{s}'-s))d\xi ds) \times \int_0^{+\infty}\int_{a_1}^{a_2} G(\xi,s)d\xi ds\Big] d\theta dyd\hat{s}' \\ >& 0, \ \forall\ x\in\mathbb{R}, \end{aligned}$$

where

$$\Gamma(x,t) := \frac{1}{\sqrt{4D\pi t}} e^{-\frac{x^2}{4Dt} - (M+\gamma_1)t}.$$

Then ,

$$U(x,t;\phi) \geq \int_{\mathbb{R}} \Gamma(x-y,t-\tau)U(y,\tau;\phi)dy + \int_s^t \int_{\mathbb{R}} \Gamma(x-y,t-\hat{s})J_2(y,\hat{s})dyd\hat{s}, \ \forall\ x\in\mathbb{R},\ t>\tau.$$

By the integral form of the second equation of (1.5), we obtain

$$V(x,t;\phi) = e^{-\gamma_2 t}\phi_2(x,0) + \gamma_1 \int_0^t e^{-\gamma_2(t-\hat{s})} U(x,\hat{s};\phi)d\hat{s} > 0, \ \forall\ x\in\mathbb{R}, t>\tau.$$

If $\phi_2(x,0) \geq 0$ with $\phi_2(x,0) \not\equiv 0$, then

$$V(x,t;\phi) = e^{-\gamma_2 t}\phi_2(x,0) + \gamma_1 \int_0^t e^{-\gamma_2(t-\hat{s})}U(x,\hat{s};\phi)d\hat{s} \geq 0(\not\equiv 0),\ \forall\ x \in \mathbb{R}, t \geq 0.$$

Since

$$V(x,t;\phi) \geq \gamma_2 \int_0^t \int_{\mathbb{R}} \Gamma(x-y,t-\hat{s})V(y,\hat{s};\phi)dyd\hat{s} \geq 0(\not\equiv 0),\ \forall\ x \in \mathbb{R}, t > 0.$$

Hence, by [24, Theorem 1.4.5], we get $U(x,t;\phi) > 0,\ \forall\ x \in \mathbb{R}, t > 0$. It then follows that $V(x,t;\phi) > 0,\ \forall\ x \in \mathbb{R}, t > 0$. Therefor, $W(x,t;\phi) \gg 0,\ \forall\ x \in \mathbb{R}, t > \tau$ and hence, $Q_t(\phi) \gg 0,\ \forall\ t > 2\tau$.

Since Q_t is sub-homogeneous, we can choose the number r_σ in [16, Theorem 2.17(ii)] to be the number $\bar{r}$, so that $r_\sigma = \bar{r}$ is independent of $\sigma \gg \mathbf{0}$. If $\phi \in \mathcal{C}_{\mathbf{K}}$ and $\phi(x,\theta) \gg 0$ for all x on an interval I of length $2\bar{r}$ and $\theta \in [-\tau, 0]$, then there exists a vector $\sigma \gg \mathbf{0}$ in $\mathbb{R}^2$ such that $\phi(x,\theta) \gg \sigma, \forall (x,\theta) \in I \times [-\tau, 0]$, and hence, [16, Theorem 2.17(ii)] implies that

$$\lim_{t\to\infty, |x|\leq ct} W(x,t;\phi) = \mathbf{K}.$$

By the claim, we can fix $t_0 > 2\tau$ such that $U_{t_0}(\phi) \gg 0$ for any given $\phi = (\phi_1, \phi_2) \in \mathcal{C}_{\mathbf{K}}$ with either $\phi_1 \not\equiv 0$ or $\phi_2(\cdot, 0) \not\equiv 0$. By taking U_{t_0} as a new initial data, we see that statement (ii) is satisfied. ☐

Now, we look for the existence of nontrivial traveling wave solutions $(U(x,t), V(x,t)) = (\phi_c(x + ct), \psi_c(x+ct))$ of (1.5) satisfying the following condition

$$(\phi_c(-\infty), \psi_c(-\infty)) = \mathbf{0},\ (\phi_c(+\infty), \psi_c(+\infty)) = \mathbf{K}. \tag{2.4}$$

Let $\xi = x + ct$, then $(\phi_c(\xi), \psi_c(\xi))$ satisfies

$$\begin{cases} c\phi_c'(\xi) = D\phi_c''(\xi) + F(\phi_c(\xi), \int_0^{+\infty}\int_{\mathbb{R}} G(y,s)B(\phi_0(\xi - y - cs))dyds) - \gamma_1\phi_c(\xi) + \gamma_2\psi_c(\xi), \\ c\psi_c'(\xi) = \gamma_1\phi_c(\xi) - \gamma_2\psi_c(\xi). \end{cases} \tag{2.5}$$

For $\lambda \geq 0$ and $c > 0$, define a function as follows

$$\begin{aligned} \Delta(c,\lambda) =& D\lambda^2 - c\lambda + \partial_1 F(0,0) \\ &+ \partial_2 F(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\lambda(y+cs)}dyds - \gamma_1 + \frac{\gamma_1\gamma_2}{c\lambda + \gamma_2}. \end{aligned} \tag{2.6}$$

Then we have the following results.

Lemma 2.5. *Assume (A1)-(A3) and (A5) hold. There exists a positive pair (c_*, λ_*) such that*

$$\Delta(c_*, \lambda_*) = 0, \quad \frac{\partial \Delta(c_*, \lambda_*)}{\partial \lambda} = 0.$$

Furthermore,

(i) *if $0 < c < c_*$, then $\Delta(c,\lambda) > 0$ for all $\lambda \in [0, \lambda_0)$;*
(ii) *if $c > c_*$, then $\Delta(c,\lambda) = 0$ has two positive real roots $\lambda_1 := \lambda_1(c)$ and $\lambda_2 := \lambda_2(c)$ with $\lambda_1(c) < \lambda_* < \lambda_2(c)$ such that*

$$\Delta(c,\cdot) > 0 \ \mathit{in}\ \mathbb{R} \setminus (\lambda_1(c), \lambda_2(c)),\ \Delta(c,\cdot) < 0\ \mathit{in}\ (\lambda_1(c), \lambda_2(c)).$$

Proof. Note Note that $\partial_1 F(0,0) < 0$ and $\partial_1 F(0,0) + \partial_2 F(0,0)B'(0) > 0$. By direct calculation, we get

$$\begin{aligned}
&\Delta(c,0) = \partial_1 F(0,0) + \partial_2 F(0,0)B'(0) > 0,\\
&\Delta(+\infty,\lambda) = -\infty,\ \forall\ \lambda \in [0,\lambda_0),\\
&\lim_{\lambda\to\lambda_0^-} \Delta(c,\lambda) = +\infty,\ \forall\ c > 0,\\
&\Delta(0,\lambda) = D\lambda^2 + \partial_1 F(0,0) + \partial_2 F(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\lambda y}dyds > 0.
\end{aligned}$$

Moreover, for $\forall\ \lambda \in (0,\lambda_0)$, we have

$$\begin{aligned}
\frac{\partial\Delta(c,0)}{\partial\lambda} =& -c\left[1 + \partial_2 F(0,0)B'(0)\int_0^{\infty}\int_{\mathbb{R}} G(y,s)sdyds + \frac{\gamma_1}{\gamma_2}\right] < 0,\\
\frac{\partial\Delta(c,\lambda)}{\partial c} =& -\lambda\left[1 + \partial_2 F(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)se^{-\lambda(y+cs)}dyds + \frac{\gamma_1\gamma_2}{(c\lambda+\gamma_2)^2}\right] < 0,\\
\frac{\partial^2\Delta(c,\lambda)}{\partial\lambda^2} =& 2D + \partial_2 F(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)(y+cs)^2 e^{-\lambda(y+cs)}dyds + \frac{2c^2\gamma_1\gamma_2}{(c\lambda+\gamma_2)^3} > 0.
\end{aligned}$$

Define

$$c_* := \inf\{c > 0 : \Delta(c,\lambda) = 0 \text{ for some } \lambda \in (0,\lambda_0)\}.$$

We can clearly see $c_* > 0$ and $\Delta(c_*,\lambda(c_*)) = 0$.

Now we claim that $\lambda(c_*)$ is uniquely determined. Otherwise, there exist $(c_*,\lambda_1(c_*))$ and $(c_*,\lambda_2(c_*))$ with $\lambda_1(c_*) < \lambda_2(c_*)$ such that

$$\Delta(c_*,\lambda_1(c_*)) = 0 \text{ and } \Delta(c_*,\lambda_2(c_*)) = 0.$$

Since $\Delta(c,\lambda)$ is strictly convex down for each $c > 0$, we have

$$\Delta(c_*,\theta\lambda_1(c_*) + (1-\theta)\lambda_2(c_*)) < \theta\Delta(c_*,\lambda_1(c_*)) + (1-\theta)\Delta(c_*,\lambda_2(c_*)) = 0, \quad \theta \in (0,1).$$

Choose a $\hat\lambda \in (\lambda_1(c_*),\lambda_2(c_*))$ and then $\Delta(c_*,\hat\lambda) < 0$. Since $\Delta(0,\hat\lambda) > 0$, and $\frac{\partial\Delta(c,\lambda)}{\partial c} < 0$ for any $\lambda \in (0,\lambda_0)$, it follows from the intermediate value theorem that there is a unique $\hat c \in (0,c_*)$ such that $\Delta(\hat c,\hat\lambda) = 0$, which contradicts the definition of c_*. Thus, the claim holds.

Moreover, it is easy to see that $\frac{\partial\Delta(c_*,\lambda_*)}{\partial\lambda} = 0$, where $\lambda_* := \lambda(c_*)$. Combining the above properties of the function $\Delta(c,\lambda)$, the conclusion follows. □

Remark 2.1. By using the linear operators approach (see [16, Theorem 3.10]), we can show that c^* in Theorem 2.3 is coincident with c_* in Lemma 2.5, i.e., $c^* = c_*$. In the remainder of the paper, we will use c^* instead of c_*.

Following the idea in [18, Theorem 2.2], the existence of solutions of (2.5) can be reduced to the existence of a pair of super-solution and sub-solution of (2.5). By Lemma 2.5, we will construct a pair of super-solution and sub-solution of (2.5). For the convenience of notational, we define

$$(G**\phi)(x) := \int_0^{\infty}\int_{\mathbb{R}} G(y,s)\phi(x-y-cs)dyds,\ \forall\ \phi \in C(\mathbb{R}).$$

From [3] we can have the following results.

Lemma 2.6. *Let $(A1)-(A3)$ and $(A5)$ hold, $c > c^*, q > 0$ and $\mu \in (1,\min\{2,\lambda_2/\lambda_1\})$. Define*

$$\phi_c^+(\xi) = \begin{cases} e^{\lambda_1\xi}, & \xi < d_1^+,\\ K, & \xi \ge d_1^+,\end{cases} \quad \psi_c^+(\xi) = \begin{cases} n(c)e^{\lambda_1\xi}, & \xi < d_2^+,\\ \bar K, & \xi \ge d_2^+,\end{cases}$$

and

$$\phi_c^-(\xi)\begin{cases} e^{\lambda_1\xi}-qe^{\mu\lambda_1\xi}, & \xi<d_1^-,\\ 0, & \xi\ge d_1^-,\end{cases}\quad \psi_c^-(\xi)\begin{cases} n(c)e^{\lambda_1\xi}-qZ(c,\mu)e^{\mu\lambda_1\xi}, & \xi<d_2^-,\\ 0, & \xi\ge d_2^-,\end{cases}$$

where $\Phi_c^+(\xi):=\big(\phi_c^+(\xi),\psi_c^+(\xi)\big),\Phi_c^-(\xi):=\big(\phi_c^-(\xi),\psi_c^-(\xi)\big)$, $n(c)=\gamma_1/(c\lambda_1+\gamma_2)$, $Z(c,\mu)=\gamma_1/(c\mu\lambda_1+\gamma_2)$, $d_1^+:=(\ln K)/\lambda_1$, $d_2^+:=(\ln\bar{K}-\ln n(c))/\lambda_1$, $d_1^-:=-(\ln q)/(\mu-1)\lambda_1$, $d_2^-:=-[\ln qZ(c,\mu)-\ln n(c)]/(\mu-1)\lambda_1$. *Then* $\Phi_c^+(\xi)$ *is a super-solution of* (2.5)*, and* $\Phi_c^-(\xi)$ *is a sub-solution of* (2.5) *provided* $q>\max\{1,n(c)/Z(c,\mu)\}$ *is large enough.*

Proof. For convenience, we denote

$$\begin{aligned} Q_1(\phi,\psi)(\xi)=&c\phi'(\xi)-D\phi''(\xi)-F(\phi(\xi),(G**B(\phi))(\xi))+\gamma_1\phi(\xi)-\gamma_2\psi(\xi),\\ Q_2(\phi,\psi)(\xi)=&c\psi'(\xi)-\gamma_1\phi(\xi)+\gamma_2\psi(\xi).\end{aligned}$$

When $\Phi'(\xi+)\le\Phi'(\xi-)$ (or $\Phi'(\xi+)\ge\Phi'(\xi-)$) for $\xi\in\mathbb{R}$, then $\Phi(\xi):=(\phi(\xi),\psi(\xi))$ is a super-solution (or sub-solution) of (2.5), and there exist $d_1,\cdots,d_m\in\mathbb{R}$ such that

$$Q_i(\phi,\psi)(\xi)\ge 0 \text{ (or } Q_i(\phi,\psi)(\xi)\le 0) \text{ for } \xi\in\mathbb{R}\backslash\{d_1,\cdots,d_m\}, i=1,2,$$

where $\Phi'(\xi+)$ and $\Phi'(\xi-)$ are the right-hand derivative and the left-hand derivative of Φ at ξ, respectively.

Step 1: We proof that $\Phi_c^+(\xi)$ is a super-solution of (2.5). By direct calculation $0<d_1^+<d_2^+$. obviously, $\Phi_c'^+(\xi+)\le\Phi_c'^+(\xi-)$ for $\xi\in\mathbb{R}$. Thus, it needs to show that $Q_i(\Phi_c^+)(\xi)\ge 0$ for $\xi\in\mathbb{R}\backslash\{d_1^+,d_2^+\}, i=1,2$.

For $\xi>d_1^+$, we have

$$\begin{aligned} Q_1(\Phi_c^+)(\xi)=&-F(K,(G**B(\Phi_c^+))(\xi))+\gamma_1K-\gamma_2\\ \ge&-F(K,B(K))+\gamma_1K-\gamma_2\bar{K}=0.\end{aligned}\tag{2.7}$$

For $\xi<d_1^+$, using the $B(U)\le B'(0)U$ for $U\in[0,K]$, we have

$$\begin{aligned} Q_1(\Phi_c^+)(\xi)\ge&e^{\lambda_1\xi}(c\lambda_1-D\lambda_1^2+\gamma_1-\gamma_2n(c))-F(\Phi_c^+,(G**B(\Phi_c^+))(\xi))\\ \ge&e^{\lambda_1\xi}\Big[c\lambda_1-D\lambda_1^2+\gamma_1-\gamma_2n(c)-\partial_1F(0,0)\\ &-\partial_2F(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}}G(y,s)e^{-\lambda(y+cs)}dyds\Big]\\ =&0.\end{aligned}\tag{2.8}$$

For $\xi>d_2^+$, we have

$$Q_2(\Phi_c^+)(\xi)=-\gamma_1\phi_c^+(\xi)+\gamma_2\bar{K}\ge-\gamma_1K+\gamma_2\bar{K}=0.\tag{2.9}$$

For $\xi<d_2^+$, we have

$$\begin{aligned} Q_2(\Phi_c^+)(\xi)=&e^{\lambda_1\xi}(c\lambda_1n(c)+\gamma_2n(c))-\gamma_1(\phi_c^+)(\xi)\\ \ge&e^{\lambda_1\xi}(c\lambda_1n(c)+\lambda_1n(c)-\gamma_1)=0.\end{aligned}\tag{2.10}$$

From (2.7)-(2.10), it is proved that $\Phi_c^+(\xi)$ is a super-solution of (2.5).

Step 2: We proof that $\Phi_c^-(\xi)$ is a sub-solution of (2.5). By direct calculation $d_1^-<d_2^-<0$. $q>n(c)/Z(c,\mu)$ has been provided before is large enough, obviously, $\Phi_c'^+(\xi+)\le\Phi_c'^+(\xi-)$ for $\xi\in\mathbb{R}$. Thus, it needs to show that $Q_i\left(\Phi_c^-\right)(\xi)\le 0$ for all $\xi\in\mathbb{R}\setminus\{d_1^-,d_2^-\},\ i=1,2$.

For $\xi>d_1^-$, we have

$$Q_1\left(\Phi_c^-\right)(\xi)=-F\left(0,\left(G**B\left(\phi_c^-\right)\right)(\xi)\right)-\gamma_2\psi_c^-(\xi)\le-\gamma_2\psi_c^-(\xi)\le 0.$$

We now consider the case $\xi < \xi_1^- < 0$. It is easy to see that

$$e^{\lambda_1 \xi} \geq \phi_c^-(\xi) \geq e^{\lambda_1 \xi} - q e^{\mu\lambda_1 \xi},\ \xi \in \mathbb{R}. \tag{2.11}$$

By using the Taylor's formula, there exist positive constants D_1 and D_2 such that

$$F(U,V) \geq \partial_1 F(0,0)U + \partial_2 F(0,0)V - D_1U^2 - D_2V^2, \tag{2.12}$$

for $U, V \in [0,K] \times [0, B(K)]$.

Since $B''(0)$ exists, there is $D_3 > 0$ such that

$$B(U) \geq B'(0)U - D_3U^2,\ \text{for } U \in [0,K]. \tag{2.13}$$

For $\xi < d_1^- < 0$, in view of (2.11)-(2.13), we have

$$\begin{aligned}
&Q_1(\Phi_c^-)(\xi)\\
=&e^{\lambda_1\xi}(c\lambda_1 - D\lambda_1 + \gamma_1 - \gamma_2 n(c)) - qe^{\mu\lambda_1\xi}(c\mu\lambda_1 - D(\mu\lambda_1)^2 + \gamma_1 - \gamma_2 Z(c,\mu))\\
&- F(\phi_c^-(\xi), (G**B(\phi_c^-))(\xi))\\
\leq&e^{\lambda_1\xi}\Big[c\lambda_1 - D\lambda_1 + \gamma_1 - \partial_1F(0,0)\\
&- \partial_2F(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\lambda_1(y+cs)}dyds - \gamma_2 n(c)\Big]\\
&- qe^{\mu\lambda_1\xi}\Big[c\mu\lambda_1 - D(\mu\lambda_1)^2 + \gamma_1 - \partial_1F(0,0)\\
&- \partial_2(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\mu\lambda_1(y+cs)}dyds - \gamma_2 Z(c,\mu)\Big] + \tilde{M}e^{2\lambda_1\xi}\\
=&-qe^{\mu\lambda_1\xi}\Big[c\mu\lambda_1 - D(\mu\lambda_1)^2 + \gamma_1 - \partial_1F(0,0)\\
&- \partial_2(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\mu\lambda_1(y+cs)}dyds - \gamma_2 Z(c,\mu)\Big] + \tilde{M}e^{2\lambda_1\xi}\\
\leq&e^{\mu\lambda_1\xi}\{-q[c\mu\lambda_1 - D(\mu\lambda_1)^2 + \gamma_1 - \partial_1F(0,0)\\
&- \partial_2(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\mu\lambda_1(y+cs)}dyds - \gamma_2 Z(c,\mu)] + \tilde{M}\}\\
\leq&0,
\end{aligned}$$

where

$$\begin{aligned}
\tilde{M} = D_1 + D_2(B'(0))^2\left(\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\lambda_1(y+cs)}dyds\right)^2\\
+D_3\partial_2F(0,0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-2\lambda_1(y+cs)}dyds > 0.
\end{aligned}$$

Similarly, for $\xi > d_2^-$, we have

$$Q_2\left(\Phi_c^-\right)(\xi) = -\gamma_1\phi_c^-(\xi) \leq 0.$$

For $\xi < d_2^-$, then

$$\begin{aligned}
&Q_2\left(\Phi_c^-\right)(\xi)\\
=&c\left[n(c)\lambda_1 e^{\lambda_1\xi} - qZ(c,\mu)\mu\lambda_1 e^{\mu\lambda_1\xi}\right] - \gamma_1\phi_c^-(\xi) + \gamma_2\left[n(c)e^{\lambda_1\xi} - qZ(c,\mu)\mu\lambda_1 e^{\mu\lambda_1\xi}\right]\\
\leq&e^{\lambda_1\xi}\left[c\lambda_1 n(c) - \gamma_1 + \gamma_2 n(c)\right] - qe^{\mu\lambda_1\xi}\left[cZ(c,\mu)\mu\lambda_1 - \gamma_1 + \gamma_2 Z(c,u)\right] = 0.
\end{aligned}$$

Therefore, $\Phi_c^-(\xi)$ is a sub-solution of (2.5).

□

With the aid of the upper and lower solutions of (2.5), we can obtained the existence and non existence of the following traveling wave solutions of (1.5).

Theorem 2.7. *Assume (A1)-(A3) and (A5) hold. Then the following result holds.*

(i) *For each $c \geq c^*$, system (1.5) has a traveling wave front $\Phi_c(\xi) := (\phi_c(\xi), \psi_c(\xi))$, which satisfies (2.4) and $\Phi_c(\xi) \gg \mathbf{0}$ for all $\xi \in \mathbb{R}$. Moreover, if $c > c^*$, then*

$$\lim_{\xi \to -\infty} \Phi_c(\xi) e^{-\lambda_1 \xi} = (1, n(c)) \text{ and } \Phi(\xi) \leq e^{\lambda_1 \xi}(1, n(c)) \text{ for all } \xi \in \mathbb{R}. \tag{2.14}$$

(ii) *For $0 < c < c^*$, system (1.5) has no traveling wave solutions connecting $\mathbf{0}$ and $\mathbf{K}$.*

Proof. By Lemma 2.6 and [18, Theorem 2.2] (or [11, Theorem 1.1]), we can prove the existence of monotone traveling wave solutions with speed $c > c^*$. From the constructions of the super-solution and sub-solution, it is easy to verify that (2.14) holds. Moreover, a limiting argument similar to that of [11, Theorem 1.1] gives the existence of the traveling wave with the wave speed c^*. The non-existence of traveling wave solutions is a direct consequence of Theorem 2.3. This completes the proof. □

Theorems 2.3 and 2.7 show that c^* is not only the spreading speed but also the minimal wave speed when (1.5) is quasi-monotone.

3. Spreading speed

This section aims at proving the nonexistence of non-quasi-monotone traveling wave solutions of system (1.5) and analyzes the upward convergence of the spreading speed. For convenience, we denote $\mathbf{K}^{\pm} = (K^{\pm}, \bar{K}^{\pm})$ and $[\mathbf{0}, \mathbf{K}^{\pm}] = [0, K^{\pm}] \times [0, \bar{K}^{\pm}]$, where $\gamma_2 \bar{K}^{\pm} = \gamma_2 K^{\pm}$.

According to (A4), we establish two auxiliary monotone delayed systems:

$$\begin{cases} U_t = & DU_{xx} + F^+(U(x,t), (G**B^+(U))(x,t)) - \gamma_1 U(x,t) + \gamma_2 V(x,t), \\ V_t = & \gamma_1 U(x,t) - \gamma_2 V(x,t), \end{cases} \tag{3.1}$$

and

$$\begin{cases} U_t = & DU_{xx} + F^-(U(x,t), (G**B^-(U))(x,t)) - \gamma_1 U(x,t) + \gamma_2 V(x,t), \\ V_t = & \gamma_1 U(x,t) - \gamma_2 V(x,t), \end{cases} \tag{3.2}$$

Recalling $\partial_1 F^{\pm} \in C(\bar{I}, \mathbb{R})$, let

$$L := \max \left\{ \max_{(U,V) \in \bar{I}} |\partial_1 F^+(U,V)|, \max_{(U,V) \in \bar{I}} |\partial_1 F^-(U,V)| \right\}. \tag{3.3}$$

For any $\phi = (\phi_1, \phi_2) \in \mathcal{C}_{\mathbf{K}^+}$, we define $H(\phi) = (H_1(\phi), H_2(\phi))$ by

$$\begin{aligned} H_1(\phi)(x) &:= F\left(\phi_1(x,0), \int_0^{+\infty} \int_{\mathbb{R}} G(y,s) B(\phi_1(x-y,-s)) dy ds\right) + L\phi_1(x,0) + \gamma_2 \phi_2(x,0), \\ H_2(\phi)(x) &:= \gamma_1 \phi_1(x,0). \end{aligned}$$

Similarly, we define $H^{\pm}(\phi) = (H_1^{\pm}(\phi), H_2^{\pm}(\phi))$ by

$$\begin{aligned} H_1^{\pm}(\phi) :=& F^{\pm}\left(\phi_1(x,0), \int_0^{+\infty} \int_{\mathbb{R}} G(y,s) B^{\pm}(\phi_1(x-y,-s)) dy ds\right) + L\phi_1(x,0) + \gamma_2 \phi_2(x,0), \\ H_2^{\pm}(\phi) :=& \gamma_1 \phi_1(x,0). \end{aligned}$$

It is clear that $H^{\pm}(\cdot)$ is monotone in $\mathcal{C}_{\mathbf{K}^+}$ and

$$H^-(\phi) \leq H(\phi) \leq H^{\pm}(\phi), \ \forall \ \phi \in \mathcal{C}_{\mathbf{K}^+}.$$

We start with the well-posedness for the initial-value problems of (1.5).

Lemma 3.1. *For any $\varphi \in \mathcal{C}_{\mathbf{K}^+}$, system (1.5) has a unique mild solution $W(x,t;\varphi)$ with $W(x,\hat{s};\varphi) = \varphi(x,\hat{s})$ for $(x,\hat{s}) \in \mathbb{R} \times [-\tau, 0]$ and $\mathbf{0} \le W(x,t;\varphi) \le \mathbf{K}^+$ for $(x,t) \in \mathbb{R} \times \mathbb{R}_+$.*

Proof. Let $\bar{I} = [0, K^+] \times [0, B^+(K^+)]$ and

$$\hat{L} := \max\left\{ \max_{(u,v)\in \bar{I}} |\partial_1 F(u,v)|, \max_{(u,v)\in \bar{I}} |\partial_2 F(u,v)| \max_{u\in[0,K^+]} |B'(u)| \right\}.$$

Consider the initial value problem

$$\begin{cases} W(x,t) = \hat{T}(t)W(\cdot,0)(x) + \int_0^t \hat{T}(t-\hat{s})H(W_{\hat{s}})(x)d\hat{s}, & \forall\ x \in \mathbb{R}, t > 0, \\ W(x,\hat{s}) = \varphi(x,\hat{s}), & x \in \mathbb{R}, \hat{s} \in [-\tau, 0]. \end{cases}$$

where $\hat{T}(t) = \mathrm{diag}(\hat{T}_1(t), \hat{T}_2(t))$ with $\hat{T}(0) = I$ and

$$\begin{aligned} \hat{T}_1(t)\phi(x) :=& e^{-(L+\gamma_1)t} \int_{\mathbb{R}} \frac{1}{\sqrt{4\pi D t}} e^{-\frac{(x-y)^2}{4Dt}} \phi(y)\, dy, \\ \hat{T}_2(t)\phi(x) :=& e^{-\gamma_2 t}\phi(x), \end{aligned}$$

for any $\phi \in BUC(\mathbb{R}, \mathbb{R})$ and $t > 0$. Let

$$\mathcal{D} := \{W \in C(\mathbb{R} \times \mathbb{R}_+, [\mathbf{0}, \mathbf{K}^+]) : W(x,t) = \varphi(x,t) \text{ for } (x,t) \in \mathbb{R} \times [-\tau, 0]\}.$$

Define an operator P on $\mathcal{D}$ by

$$P(W)(x,t) = \begin{cases} \hat{T}(t)W(\cdot,0)(x) + \int_0^t \hat{T}(t-\hat{s})H(W_{\hat{s}})(x)d\hat{s}, & x \in \mathbb{R}, t > 0, \\ \varphi(x,t), & x \in \mathbb{R}, t \in [-\tau, 0]. \end{cases}$$

Note that $\hat{T}(t)(\cdot)$ is a positive operator and monotone on $\mathcal{D}, \forall t \ge 0$. Then,

$$\begin{aligned} 0 \le& \hat{T}_1(t)\varphi_1(\cdot,0)(x) + \int_0^t \hat{T}_1(t-\hat{s})H_1(W_{\hat{s}})(x)d\hat{s} \\ \le& \hat{T}_1(t)K^+ + \int_0^t \hat{T}_1(t-\hat{s})H_1^+(K^+)(x)d\hat{s} \\ =& K^+, \end{aligned}$$

and

$$\begin{aligned} 0 \le& \hat{T}_2(t)\varphi_2(\cdot,0)(x) + \int_0^t \hat{T}_2(t-\hat{s})H_2(W_{\hat{s}})(x)d\hat{s} \\ \le& \hat{T}_2(t)K^+ + \int_0^t \hat{T}_2(t-\hat{s})H_2^+(K^+)(x)d\hat{s} \\ =& \bar{K}^+, \end{aligned}$$

which implies $P(\mathcal{D}) \subset \mathcal{D}$. For $\mu > 0$, define

$$\begin{aligned} \|W\|_\mu :=& \max\left\{ \sup_{x\in\mathbb{R}, t\ge 0} |W_1(x,t)|e^{-\mu t}, \sup_{x\in\mathbb{R}, t\ge 0} |W_2(x,t)|e^{-\mu t} \right\}, \\ d_\mu(U,V) :=& \|U - V\|_\mu,\ \forall\ U, V \in \mathcal{D}. \end{aligned}$$

Then $(\mathcal{D}, d_\mu)$ is a complete metric space. For any $U=(U_1,U_2), V=(V_1,V_2)\in\mathcal{D}$, we have

$$\begin{aligned}
&|H_1(U_t)(x)-H_1(V_t)(x)|e^{-\mu t}\\
\le\ & L|U_1(x,t)-V_1(x,t)|e^{-\mu t}+\gamma_2|U_2(x,t)-V_2(x,t)|e^{-\mu t}\\
&+\left|\partial_1 F\left(\eta_1(x,t),\int_0^{+\infty}\int_{\mathbb{R}}G(y,s)B(U_1(x-y,t-s))\,dyds\right)\right||U_1(x,t)-V_1(x,t)|e^{-\mu t}\\
&+|\partial_2 F(V_1(x,t),\eta_2(x,t))|\\
&\times\int_0^{+\infty}\int_{\mathbb{R}}G(y,s)|B'(\eta_3(x-y,t-s))||U_1(x-y,t-s)-V_1(x-y,t-s)|e^{-\mu t}dyds\\
\le&(2\hat{L}+L+\gamma_2)\|U-V\|_\mu,\ \forall\ x\in\mathbb{R}, t\ge 0,
\end{aligned}$$

and

$$|H_2(U_t)(x)-H_2(V_t)(x)|e^{-\mu t}\le\gamma_1\|U-V\|_\mu,\ \forall\ x\in\mathbb{R}, t\ge 0,$$

where

$$\begin{aligned}
\eta_1(x,t)=&\theta_1U_1(x,t)+(1-\theta_1)V_1(x,t),\\
\eta_2(x,t)=&\theta_2\int_0^{+\infty}\int_{\mathbb{R}}G(y,s)B(U_1(x-y,t-s))dyds\\
&+(1-\theta_2)\int_0^{+\infty}\int_{\mathbb{R}}G(y,s)B(V_1(x-y,t-s))dyds,\\
\eta_3(x-y,t-s)=&\theta_3U_1(x-y,t-s)+(1-\theta_3)V_1(x-y,t-s),
\end{aligned}$$

with $\theta_1,\theta_2,\theta_3\in(0,1)$. Furthermore,

$$\begin{aligned}
|P_1(U)(x,t)-P_1(V)(x,t)|e^{-\mu t}\le&\int_0^t\hat{T}(t-\hat{s})|H_1(U_{\hat{s}})(x)-H_1(V_{\hat{s}})(x)|e^{-\mu t}d\hat{s}\\
\le&\frac{2\hat{L}+L+\gamma_2}{L+\gamma_1+\mu}\|U-V\|_\mu,\ \forall\ x\in\mathbb{R},\ t>0,
\end{aligned}$$

and

$$\begin{aligned}
|P_2(U)(x,t)-P_2(V)(x,t)|e^{-\mu t}\le&\int_0^t e^{\gamma_2(t-\hat{s})}|H_2(U_{\hat{s}})(x)-H_2(V_{\hat{s}})(x)|e^{-\mu t}d\hat{s}\\
\le&\frac{\gamma_1}{\gamma_2+\mu}\|U-V\|_\mu,\ \forall\ x\in\mathbb{R},\ t>0.
\end{aligned}$$

This implies

$$\|P(U)-P(V)\|_\mu\le\max\left\{\frac{2\hat{L}+L+\gamma_2}{L+\gamma_1+\mu},\frac{\gamma_1}{\gamma_2+\mu}\right\}\|U-V\|_\mu.$$

Choose $\mu>\max\{2\hat{L}+\gamma_2-\gamma_1,\gamma_1-\gamma_2\}$, so that $\max\left\{(2\hat{L}+L+\gamma_2)/(L+\gamma_1+\mu),\gamma_1/(\gamma_2+\mu)\right\}<1$. Therefore, it is concluded that P is a compression map on $\mathcal{D}$. By using the contraction mapping theorem, P has a unique fixed point W in $\mathcal{D}$, which is the unique mild solution of (1.5) such that $W(x,t)=\phi(x,t)$, for $(x,t)\in\mathbb{R}\times[-\tau,0]$. □

Lemma 3.2 (Comparison principle)**.** *For any $\phi,\phi^+\in\mathcal{C}_{\mathbf{K}^+}$ and $\phi^-\in\mathcal{C}_{\mathbf{K}^-}$ with*

$$\phi^-(x,\hat{s})\le\phi(x,\hat{s})\le\phi^+(x,\hat{s}),\quad\forall(x,\hat{s})\in\mathbb{R}\times[-\tau,0];$$

let $W^-(x,t;\phi^-), W(x,t;\phi)$ and $W^+(x,t;\phi^+)$ be the solution of systems (3.2), (1.5) and (3.3) through ϕ^-,ϕ and ϕ^+, respectively. Then

$$W^-(x,t;\phi^-)\le W(x,t;\phi)\le W(x,t;\phi^+),\quad\forall(x,t)\in\mathbb{R}\times\mathbb{R}_+.$$

Proof. The proof is similar to that of [37, Lemma 3.1] and thus omitted. □

Now, we state the result on the spreading speed for (1.5) without quasi-monotonicity. In particular, to obtain the upward convergence of spreading speed, we further make the following assumption.

(H) $F(U,V) = -\alpha U + g(V)$ for $(U,V) \in [0,K] \times [0,B(K)]$, where $\alpha > 0$ is a constant and $g(\cdot)$ is a given function, $g(B(U))/U$ is strictly decreasing for $U \in [K^-, K^+]$, and $b(U) := \frac{1}{\alpha} g(B(U))$ satisfies:
  (P) $\forall U_1, U_2 \in [K^-, K^+]$ satisfying $U_2 \le K \le U_1, U_2 \ge b(U_1)$ and $U_1 \le b(U_2)$, there holds $U_1 = U_2$.

Theorem 3.3. *Assume that (A1)-(A4) hold. Let $W(x,t;\phi) = (U(x,t;\phi), V(x,t;\phi))$ be the unique global solution of (4) through the initial function $\phi \in \mathcal{C}_{\mathbf{K}^+}$. Then the following statements are valid:*

(i) *For any $c > c^*$, if $\mathbf{0} \le \phi \ll \mathbf{K}^+$ and $\phi(x,\cdot) = \mathbf{0}$ for x outside a bounded interval, then*

$$\lim_{t\to\infty, |x|\ge ct} W(x,t;\phi) = \mathbf{0}.$$

(ii) *For any $c \in (0, c^*)$, if $\phi := (\phi_1, \phi_2) \in \mathcal{C}_{\mathbf{K}^+}$ and either $\phi_1 \not\equiv 0$ or $\phi_2(\cdot, 0) \not\equiv 0$ holds, then*

$$\mathbf{K}^- \le \liminf_{t\to\infty, |x|\le ct} W(x,t;\phi) \le \limsup_{t\to\infty, |x|\le ct} W(x,t;\phi) \le \mathbf{K}^+.$$

Moreover, if (H) holds, then

$$\lim_{t\to\infty, |x|\le ct} W(x,t;\phi) = \mathbf{K}.$$

Proof. The proof is similar to those of [8, Theorem 3.3], [14, Theorem 2.2] and [37, Theorem 3.3]. For any $\phi \in \mathcal{C}_{\mathbf{K}^+}$, define $\tilde{\phi} \in \mathcal{C}_{\mathbf{K}^-}$ by $\tilde{\phi}(x,t) = \min\{\phi(x,t), \mathbf{K}^-\}$. From Lemma 3.2, we have

$$W^-(x,t;\tilde{\phi}) \le W(x,t;\phi) \le W^+(x,t;\phi), \ \forall x \in \mathbb{R}, t \ge 0. \tag{3.4}$$

By Theorem 2.3, c^* is the spreading speed of solutions for (3.1) and (3.2), which together with (3.4) implies that c^* satisfies the statement (i) and the first part of (ii).

Next, we prove the upward convergence of the spreading speeds by the fluctuation method (see [8, 14]). First, we simplify the notation $W(x,t;\phi) = (U(x,t;\phi), V(x,t;\phi))$ by $W(x,t) = (U(x,t), V(x,t))$. Define a function by $W(x,t) = (U(x,t), V(x,t))$. Define a function

$$J(U,V) := \begin{cases} \min\limits_{z\in[U,V]} B(z), & \text{if } U \le V, \\ \max\limits_{z\in[V,U]} B(z), & \text{if } V \le U. \end{cases}$$

Clearly, $J(U,V)$ is non-decreasing in U and non-increasing in V, and $J(U,U) = B(U)$. The integral form of (1.5) can be written as

$$
\begin{aligned}
U(x,t) =& \int_{\mathbb{R}} e^{-(\alpha+\gamma_1)t}\Gamma_0(x-y,t)U(y,0)dy \\
&+ \int_0^t \int_{\mathbb{R}} e^{-(\alpha+\gamma_1)(t-\hat{s})}\Gamma_0(y,t-\hat{s})\Big[\gamma_2 V(x-y,\hat{s}) \\
&+ g\left((G**B(U))(x-y,\hat{s})\right)\Big]dyd\hat{s} \\
=& \int_{\mathbb{R}} e^{-(\alpha+\gamma_1)t}\Gamma_0(x-y,t)U(y,0)dy \\
&+ \int_{-t}^0 \int_{\mathbb{R}} e^{-(\alpha+\gamma_1)\hat{s}}\Gamma_0(y,-\hat{s})\Big[\gamma_2 V(x-y,t+\hat{s}) \\
&+ g\left((G**J(U,U))(x-y,t+\hat{s})\right)\Big]dyds,
\end{aligned}
\tag{3.5}
$$

where

$$\Gamma_0(x,t) := \frac{1}{\sqrt{4D\pi t}}e^{-\frac{x^2}{4D\pi t}}$$

and

$$
\begin{aligned}
V(x,t) =& e^{-\gamma_2 t}V(x,0) + \gamma_1 \int_0^t e^{-\gamma_2(t-\hat{s})}U(x,\hat{s})d\hat{s} \\
=& e^{-\gamma_2 t}V(x,0) + \gamma_1 \int_t^0 e^{\gamma_2 \hat{s}}U(x,t+\hat{s})d\hat{s}.
\end{aligned}
\tag{3.6}
$$

For any $\beta \in (0, c*)$, define

$$
\begin{aligned}
U_*(\nu) = \liminf_{t\to\infty,|x|\le\nu t} U(x,t) \text{ and } U^*(\nu) := \limsup_{t\to\infty,|x|\le\nu t} U(x,t), \\
V_*(\nu) = \liminf_{t\to\infty,|x|\le\nu t} V(x,t) \text{ and } V^*(\nu) := \limsup_{t\to\infty,|x|\le\nu t} V(x,t).
\end{aligned}
$$

Let $c \in (0, c^*)$ be given, and fix a number $\gamma \in (c, c^*)$, define

$$
\begin{aligned}
U_*(c,\gamma) = \inf_{c<\nu<\gamma} U_*(\nu) \text{ and } U^*(c,\gamma) := \sup_{c<\nu<\gamma} U^*(\nu), \\
V_*(c,\gamma) = \inf_{c<\nu<\gamma} V_*(\nu) \text{ and } V^*(c,\gamma) := \sup_{c<\nu<\gamma} V^*(\nu).
\end{aligned}
$$

For any $\nu \in (c,\gamma)$, we can choose two sequences $\{t_j\}$ in $(0,\infty)$ and$\{x_j\}$in $\mathbb{R}$ such that $|x_j| \le \nu t_j, t_j \to \infty$ as $j \to \infty$ and $\lim_{j\to\infty} U(x_j,t_j) = U_*(\nu)$. For any given $y \in \mathbb{R}$ and $\hat{s} \in \mathbb{R}_+$, we have $\liminf_{j\to\infty} V(x_j - y, t_j + \hat{s}) \ge V_*(\gamma)$ and

$$U_*(\gamma) \le \liminf_{j\to\infty} U(x_j - y, t_j + \hat{s} - \tau) \le \limsup_{j\to\infty} U(x_j - y, t_j + \hat{s} - \tau) \le U^*(\gamma).$$

By Fatou's Lemma, it follows from (3.5) that

$$
\begin{aligned}
U_*(\nu) \ge& \lim\inf_{j\to\infty} \int_{-t_j}^0 \int_{\mathbb{R}} e^{-(\alpha+\gamma_1)\hat{s}}\Gamma_0(y,-\hat{s})\Big[\gamma_2 V(x_j-y,t_j+\hat{s}) \\
&+ g\left((G**J(U,U))(x_j-y,t_j+\hat{s})\right)\Big]dyds, \\
\ge& \int_{-\infty}^0 \int_{\mathbb{R}} e^{-(\alpha+\gamma_1)\hat{s}}\Gamma_0(y,-\hat{s}) \lim\inf_{j\to\infty}\Big[\gamma_2 V(x_j-y,t_j+\hat{s}) \\
&+ g\left((G**J(U,U))(x_j-y,t_j-\hat{s})\right)\Big]dyd\hat{s} \\
\ge& \left[\gamma_2 V_*(\gamma) + g(J(U_*(\gamma),U^*(\gamma)))\right]/(\alpha+\gamma_1),
\end{aligned}
$$

which implies

$$(\alpha+\gamma_1)U_*(\nu) \geq \gamma_2 V_*(\gamma) + g(J(U_*(\gamma), U^*(\gamma))),$$

similarly, from (3.5) and (3.6) ,we have

$$\begin{aligned}&(\alpha+\gamma_1)\, U^*(\nu) \leq \gamma_2 V^*(\gamma) + g\left(J\left(U^*(\gamma), U_*(\gamma)\right)\right),\\ &\gamma_2 V_*(\nu) \geq \gamma_1 U_*(\gamma) \text{ and } \gamma_2 V^*(\nu) \leq \gamma_1 U^*(\gamma),\end{aligned}$$

it then follows that

$$\begin{aligned}&(\alpha+\gamma_1)\, U_*(c,\gamma) \geq \gamma_2 V_*(c,\gamma) + g\left(J\left(U_*(c,\gamma), U^*(c,\gamma)\right)\right),\\ &\gamma_2 V_*(c,\gamma) \geq \gamma_1 U_*(c,\gamma),\\ &(\alpha+\gamma_1)\, U^*(c,\gamma) \leq \gamma_2 V^*(c,\gamma) + g\left(J\left(U^*(c,\gamma), U_*(c,\gamma)\right)\right),\\ &\gamma_2 V^*(c,\gamma) \leq \gamma_1 U^*(c,\gamma),\end{aligned} \tag{3.7}$$

according to the definition of J, there exists $U_1, U_2 \in [U_*(c,\gamma), U^*(c,\gamma)] \subset [K^-, K^+]$ such that

$$J\left(U_*(c,\gamma), U^*(c,\gamma)\right) = B\left(U_1\right),\ J\left(U^*(c,\gamma), U_*(c,\gamma)\right) = B\left(U_2\right),$$

from (3.7), we have

$$U_*(c,\gamma) \geq \frac{1}{\alpha} g\left(B\left(U_1\right)\right) \text{ and } U^*(c,\gamma) \leq \frac{1}{\alpha} g\left(B\left(U_2\right)\right),$$

in view of assumption (H), we have

$$b\left(U_1\right) = \frac{1}{\alpha} g\left(B\left(U_1\right)\right) \leq U_*(c,\gamma) \leq U_1, U_2 \leq U^*(c,\gamma) \leq \frac{1}{\alpha} g\left(B\left(U_2\right)\right) = b\left(U_2\right),$$

and hence

$$\frac{g\left(B\left(U_1\right)\right)}{\alpha U_1} \leq 1 = \frac{g(B(K))}{\alpha K} \leq \frac{g\left(B\left(U_2\right)\right)}{\alpha U_2}$$

since $g(B(U))/U$ is strictly decreasing for $U \in [K^-, K^+]$, it follows that $U_2 \leq K \leq U_1$. The property (P) implies that $U_1 = U_2 = K$, and hence,

$$U_*(c,\gamma) = U^*(c,\gamma) = K, \tag{3.8}$$

moreover, we deduce from (3.7) and (3.8) that

$$\gamma_1 K = \gamma_1 U_*(c,\gamma) \leq \gamma_2 V_*(c,\gamma) \leq \gamma_2 V^*(c,\gamma) \leq \gamma_1 U^*(c,\gamma) = \gamma_1 K,$$

and hence $V_*(c,\gamma) = V^*(c,\gamma) = \frac{\gamma_1 K}{\gamma_2} = \bar{K}$. Consequently,

$$\begin{aligned}K =& U_*(c,\gamma) \leq U_*(c) \leq U^*(c) \leq U^*(c,\gamma) = K,\\ \bar{K} =& V_*(c,\gamma) \leq V_*(c) \leq V^*(c) \leq V^*(c,\gamma) = \bar{K},\end{aligned}$$

which imply that $\lim_{t\to\infty,|x|\leq ct} W(x,t;\phi) = \mathbf{K}$ for any $c \in (0,c^*)$. □

Theorem 3.4. *Assume that* $(A1)-(A_4)$ *hold. For any* $0 < c < c^*$, (1.5) *has no traveling wave solution* $\Phi_c(\xi)$ *with* $\liminf_{\xi\to\infty} \Phi_c(\xi) \gg \mathbf{0}$ *and* $\Phi_c(-\infty) = \mathbf{0}$.

Proof. Assume, by contradiction, that for some $c_1 \in (0,c^*)$, (1.5) has a traveling wave solution $W(x,t) = \Phi_{c_1}(x + c_1 t)$ such that $\liminf_{\xi\to\infty} \Phi_{c_1}(\xi) \gg \mathbf{0}$ and $\Phi_{c_1}(-\infty) = \mathbf{0}$. Let

$$\phi(x,\theta) := \Phi_{c_1}\left(x + c_1\theta\right),\ \forall\ \theta \in [-\tau, 0],$$

it is easy to see that $\phi_1 \not\equiv 0$ and $\phi_2(\cdot,0) \not\equiv 0$, by Theorem 3.3(ii), there holds

$$\liminf_{t\to\infty,|x|\leq ct} W(x,t;\phi) \geq \mathbf{K}^- \gg \mathbf{0},\ \forall\ c \in (0,c^*),$$

let$\bar{c} \in (c_1, c^*)$ and $x = -\bar{c}t$, then

$$\mathbf{0} = \lim_{j\to\infty} \Phi_{c_1}(-(\bar{c}-c_1)t) = \lim_{j\to\infty} W(-\bar{c}t,t) \geq \lim_{t\to\infty, |x|\leq \bar{c}t} \inf W(x,t) \gg \mathbf{0},$$

□

4. Traveling waves

In this section, we establish the existence of non-monotonic traveling waves of (1.5) by using the Schauder fixed-point theorem. Moreover, we also use the monotonicity of the traveling wave solution in the auxiliary system (3.2) to obtain the asymptotic behavior of the wave profile.

Theorem 4.1. *Assume that (A1)-(A4) hold. For each $c > c^*$, let $\lambda_1(c)$ be defined as in Lemma 2.5 and $b(c) = \frac{\gamma_1}{c\lambda_1(c)+\gamma_2}$. Then (1.5) admits a traveling wave solution $\Phi_c(\xi)$ such that*

$$\Phi_c(-\infty) = \mathbf{0},\ \mathbf{0} \ll \Phi_c(\xi) \leq \mathbf{K}^+,\ \forall\ \xi \in \mathbb{R}, \tag{4.1}$$

$$\mathbf{K}^- \leq \liminf_{\xi\to+\infty} \Phi_c(\xi) \leq \limsup_{\xi\to+\infty} \Phi_c(\xi) \leq \mathbf{K}^+ \ \textit{and} \ \lim_{\xi\to-\infty} \Phi_c(\xi)e^{-\lambda_1(c)\xi} = (1, n(c)), \tag{4.2}$$

moreover, if (H) holds, then $\lim_{\xi\to+\infty} \Phi_c(\xi) = \mathbf{K}$.

Proof. Recalling the definition of L in (3.3), we let

$$\bar{L} := \max\left\{L, \max_{(U,V)\in\bar{I}} |\partial_1 F(U,V)|, \max_{(U,V)\in\bar{I}} |\partial_2 F(U,V)|\right\},$$

and

$$r_1 = \frac{c - \sqrt{c^2 + 4D\left(\bar{L}+\gamma_1\right)}}{2D} \quad \text{and} \quad r_2 = \frac{c + \sqrt{c^2 + 4D\left(\bar{L}+\gamma_1\right)}}{2D},$$

clearly, $r_1 < 0 < r_2$ and $Dr_i^2 - cr_i - \left(\bar{L}+\gamma_1\right) = 0, i = 1, 2$. Define an operator $T = (T_1, T_2)$: $C(\mathbb{R}, [\mathbf{0}, \mathbf{K}^+]) \to C(\mathbb{R}, \mathbb{R}^2)$ by

$$\begin{aligned} T_1(\Psi)(\xi) =& \frac{1}{D(r_2-r_1)}\left[\int_{-\infty}^{\xi} e^{r_1(\xi-\hat{s})} F_1(\Psi)(\hat{s})d\hat{s} + \int_{\xi}^{+\infty} e^{r_2(\xi-\hat{s})} F_1(\Psi)(\hat{s})d\hat{s}\right], \\ T_2(\Psi)(\xi) =& \frac{1}{c}\int_{-\infty}^{\xi} e^{-\frac{\gamma_2}{c}(\xi-\hat{s})} F_2(\Psi)(\hat{s})d\hat{s}, \end{aligned} \tag{4.3}$$

where $\Psi(\xi) = (\phi(\xi), \psi(\xi))$ and

$$\begin{aligned} S_1(\Psi)(\xi) :=& \bar{L}\phi(\xi) + F(\phi(\xi), (G**B(\phi))(\xi)) + \gamma_2\psi(\xi), \\ S_2(\Psi)(\xi) :=& \gamma_1\phi(\xi), \end{aligned}$$

it is easy to verify that a fixed point of T is a solution of (2.5) (also see [25, Lemma 4.1]). Similarly, we define $T^\pm = (T_1^\pm, T_2^\pm)$ as in (4.3) with $S = (S_1, S_2)$ replaced by $S^\pm = (S_1^\pm, S_2^\pm)$, where

$$\begin{aligned} S_1^\pm(\Psi)(\xi) =& \bar{L}\phi(\xi) + F^\pm(\phi(\xi), (J**B^\pm(\phi))(\xi)) + \gamma_2\psi(\xi), \\ S_2^\pm(\Psi)(\xi) =& \gamma_1\phi(\xi), \end{aligned}$$

by (ii) of (1.5), it follows that $T^\pm(\Psi)$ is monotone, and for any $\Psi \in C(\mathbb{R}, [\mathbf{0}, \mathbf{K}^+])$,

$$T^-(\Psi) \leq T(\Psi) \leq T^+(\Psi),$$

in view of $\Delta(c, \lambda_1(c)) = 0$, we have

$$\begin{aligned} &\partial_1 F(0,0) + \partial_2 F(0,0)B'(0)\int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\lambda_1(c)(y+cs)}dyds + \frac{\gamma_1\gamma_2}{c\lambda_1(c)+\gamma_2} \\ =& -D\lambda_1^2(c) + c\lambda_1(c) + \gamma_1 > 0, \end{aligned}$$

and hence $\lambda_1(c) < r_2$. Define

$$\tilde{\Phi}^+(\xi) := \left(\min\{K^+, e^{\lambda_1(c)\xi}\}, \min\{\bar{K}^+, b(c)e^{\lambda_1(c)\xi}\}\right),$$

noting that $S^+(U,V) \le \partial_1 F(0,0)U + \partial_2 F(0,0)V$ for $(U,V) \in \bar{I}$, we deduce that $T^+(\tilde{\Phi}^+)(\xi) \le \tilde{\Phi}^+(\xi)$ for $\xi \in \mathbb{R}$. Then for a given $\lambda \in (0, \min\{\lambda_1(c), r_2\})$, let

$$X_\lambda := \{\Psi \in C(\mathbb{R}, \mathbb{R}^2) : \sup_{\xi\in\mathbb{R}} \|\Psi(\xi)\| e^{-\lambda\xi} < +\infty\},$$

with the norm $\|\Psi\|_\lambda = \sup_{\xi\in\mathbb{R}} \|\Psi(\xi)\|e^{-\lambda\xi}$. Then $(X_\lambda, \|\cdot\|_\lambda)$ is a Banach space. Since $\partial_i S^\pm(0,0) = \partial_i F(0,0),\ i = 1,2,\ \Delta(c,\lambda) = 0$ is also the characteristic equation of (3.1) and (3.2) with respect to the trivial equilibrium $\mathbf{0}$. It thus follows from Theorem 2.7 that for any $c > c^*$, (3.2) admits a non-decreasing traveling wave solution $\Phi_c^-(\xi) = (\phi_c^-(\xi), \psi_c^-(\xi)), \xi = x + c\hat{s}$ such that

$$\Phi_c^-(\cdot) \gg \mathbf{0},\ \Phi_c^-(-\infty) = \mathbf{0},\ \Phi_c^-(+\infty) = \mathbf{K}^-,$$

$$\liminf_{\xi\to-\infty} \Phi_c^-(\xi)e^{-\lambda_1(c)\xi} = (1, n(c)) \ \text{ and } \Phi_c^-(\xi) \le e^{\lambda_1(c)\xi}(1, n(c)),\ \forall\ \xi \in \mathbb{R},$$

it is easy to see that $\Phi_c^-, \tilde{\Phi}^+ \in X_\lambda$, and hence $\Omega := \left\{\Psi \in X_\lambda : \Phi_c^- \le \Psi \le \tilde{\Phi}^+\right\}$ is a nonempty, convex and closed subset of X_λ. For any $\Psi \in \Omega$, we have $\Phi_c^- = T^-(\Phi_c^-) \le T^-(\Psi) \le T(\Psi) \le T^+(\Psi) \le T^+(\tilde{\Phi}^+) \le \tilde{\Phi}^+$. and hence $T(\Omega) \subset \Omega$. Now, we prove that T is compact on Ω. We first show that T is continuous on Ω. For any $\Psi_1 = (\phi_1, \psi_1), \Psi_2 = (\phi_2, \psi_2) \in \Omega$, there holds

$$\begin{aligned}
&|S_1(\Psi_1)(\xi) - S_1(\Psi_2)(\xi)|e^{-\lambda\xi} \\
\le& \bar{L}|\phi_1(\xi) - \phi_2(\xi)|e^{-\lambda\xi} + \gamma_2|\psi_1(\xi) - \psi_2(\xi)|e^{-\lambda\xi} \\
&+ |\partial_1 F(\eta_1(\xi), (G**B(\phi_1))(\xi))||\phi_1(\xi) - \phi_2(\xi)|e^{-\lambda\xi} \\
&+ |\partial_2 F(\phi_2(\xi), \eta_2(\xi))| \int_0^{+\infty} \int_{\mathbb{R}} G(y,s) \\
&\times |B'(\eta_3(\xi - y - cs))||\phi_1(\xi - y - cs) - \phi_2(\xi - y - cs)|dyds e^{-\lambda\xi} \\
\le& \bar{L}_1\|\Psi_1 - \Psi_2\|_\lambda,
\end{aligned}$$

where $\bar{L}_1 := 2\bar{L} + \gamma_2 + \bar{L}\max_{U\in[0,K^+]}|B'(U)| \int_0^{+\infty}\int_{\mathbb{R}} G(y,s)e^{-\lambda(y+cs)}dyds$,

$$\begin{aligned}
&\eta_1(\xi) = \theta_1\phi_1(\xi) + (1-\theta_1)\,\phi_2(\xi), \\
&\eta_2(\xi) = \theta_2\,(G**B\,(\phi_1))\,(\xi) + (1-\theta_2)\,(G**B\,(\phi_2))\,(\xi), \\
&\eta_3(\xi - y - cs) = \theta_3\phi_1(\xi - y - cs) + (1-\theta_3)\,\phi_2(\xi - y - cs),
\end{aligned}$$

with $\theta_i \in (0,1), i = 1,2,3$. Then we have

$$|T_1(\Psi_1)(\xi) - T_1(\Psi_2)(\xi)|e^{-\lambda\xi} \le \frac{\bar{L}_1}{D(\lambda - r_1)(r_2 - \lambda)}\|\Psi_1 - \Psi_2\|_\lambda, \tag{4.4}$$

similarly, we obtain

$$|T_2(\Psi_1)(\xi) - T_2(\Psi_2)(\xi)|e^{-\lambda\xi} \le \frac{\gamma_1}{c\lambda + \gamma_2}\|\Psi_1 - \Psi_2\|_\lambda, \tag{4.5}$$

the inequalities (4.4) and (4.5) lead to

$$\|T(\Psi_1) - T(\Psi_2)\|_\lambda \le \frac{\bar{L}_1 + \gamma_1}{\min\{D(\lambda - r_1)(r_2 - \lambda), c\lambda + \gamma_2\}}\|\Psi_1 - \Psi_2\|_\lambda,$$

which implies that T is continuous on Ω.

Next, we show that $T:\Omega\to\Omega$ is compact with respect to the norm $\|\cdot\|_{X_\lambda}$. For any $\Psi\in\Omega$ and $\xi\in\mathbb{R}$, direct calculation yields

$$|T_1(\Psi)(\xi)|\le\frac{\tilde{L}K^++\gamma_2\tilde{K}^++\max_{(U,V)\in\tilde{I}}|F(U,V)|}{\tilde{L}+\gamma_1},\ |T_2(\Psi)(\xi)|\le\frac{\gamma_1K^+}{c},$$

$$|T_1(\Psi)'(\xi)|\le\frac{2(\tilde{L}K^++\gamma_2\tilde{K}^++\max_{(U,V)\in\tilde{I}}|F(U,V)|)}{D(r_2-r_1)},\ |T_2(\Psi)'(\xi)|\le\frac{\gamma_1K^+(\gamma_2+c)}{c^2}.$$

Therefore, the family of functions $\{T(\Psi)(\xi):\Psi\in\Omega\}$ is uniformly bounded and equicontinuous in $\xi\in\mathbb{R}$. By means of the method in [3, Theorem 3.1], we can prove that $T(\Omega)$ is compact in X_λ. As a consequence, Schauder's fixed point theorem implies that T has a fixed point Φ_c in Ω, which is a traveling wave solution of (4) for $c>c^*$. Since

$$\mathbf{0}<\Phi_c(\xi)\le\Phi_c^+(\xi)\le\tilde{\Phi}_c^+(\xi),\ \forall\xi\in\mathbb{R},$$

it follows that (4.1) and (4.2) hold. Finally, when (H) holds, by using similar arguments as in the proof of [31, Theorem 2.4], one obtains that $\lim_{\xi\to+\infty}\Phi_c(\xi)=\mathbf{K}$. □

Theorem 4.2. *Assume that (A1)-(A4) hold and $c=c^*$. For any vector $\sigma\gg\mathbf{0}$ with $\|\sigma\|<1$, (1.5) admits a non-constant traveling wave solution $\Phi_*(\xi)$ such that*

$$\Phi_*(\xi)\le\sigma,\ \forall\ \xi\le0\quad \textit{and } 0\le\Phi_*(\xi)\le\mathbf{K}^+,\ \forall\xi\in\mathbb{R},\tag{4.6}$$

$$\mathbf{K}^-\le\liminf_{\xi\to+\infty}\Phi_*(\xi)\le\limsup_{\xi\to+\infty}\Phi_*(\xi)\le\mathbf{K}^+.\tag{4.7}$$

Moreover, $\Phi_*(-\infty)=\mathbf{0}$ and if (H) holds, then $\lim_{\xi\to+\infty}\Phi_*(\xi)=\mathbf{K}$.

Proof. We use similar arguments as [8, Theorem 4.2] and [26, Theorem 4.13]. Choose a sequence $\{c_j\}\subset(c^*,+\infty)$ such that $\lim_{j\to\infty}c_j=c^*$. By Theorem 4.1, there exists a traveling wave (Φ_j,c_j) of (1.5) for each j such that

$$\mathbf{K}^-\le\liminf_{\xi\to+\infty}\Phi_j(\xi)\le\limsup_{\xi\to+\infty}\Phi_j(\xi)\le\mathbf{K}^+.$$

Given any $\sigma\gg\mathbf{0}$ with $\|\sigma\|\ll1$. Since $\Phi_j(\xi+h),h\in\mathbb{R}$, is also a solution satisfying $\Phi_j(-\infty)=\mathbf{0}$, we can assume that $\Phi_j(\xi)\le\sigma$ for $\xi\le0$. Similar to the proof of Theorem 4.1, we can prove that the family of functions $\{\Phi_j(\xi)\}_{j=1}^{\infty}$ is uniformly bounded and equi-continuous on $\mathbb{R}$. Thus, there exists a subsequence of $\{c_j\}$, still denoted by $\{c_j\}$, such that $\Phi_j(\xi)$ converges uniformly on every bounded interval, and hence pointwise on $\mathbb{R}$ to a function $\Phi_*(\xi):=(\phi_*(\xi),\psi_*(\xi))$. Note that $\Phi_j(\xi)=T(\Phi_j)(\xi),\ \xi\in\mathbb{R}$. Letting $j\to\infty$ in the above equation and using the dominated convergence theorem, we get $\Phi_*(\xi)=T(\Phi_*)(\xi)$ for $\xi\in\mathbb{R}$, and hence, (4.6) and (4.7) hold.

Next, we show that $\Phi_*(-\infty)=\mathbf{0}$. We first prove that

$$\int_{-\infty}^0\phi_*(\xi)\,d\xi<+\infty \text{ and } \int_{-\infty}^0\psi_*(\xi)\,d\xi<+\infty,\tag{4.8}$$

it is easy to define that for any $\varepsilon>0$ satisfying

$$(\partial_1F(0,0)-\varepsilon)+(\partial_2F(0,0)-\varepsilon)(B'(0)-\varepsilon)>0 \text{ and } \partial_2F(0,0)-\varepsilon>0,$$

there exists $\delta_i(\varepsilon)=\delta_i>0,\ i=1,2,3$, such that the following inequality holds

$$\begin{aligned}F(U,V)&\ge(\partial_1F(0,0)-\varepsilon)U+(\partial_2F(0,0)-\varepsilon)V,\ \forall\ (U,V)\in[0,\delta_1]\times[0,\delta_2],\\ B(U)&\ge(B'(0)-\varepsilon)U,\ \forall\ U\in[0,\delta_3],\end{aligned}$$

denote ρ_1 and ρ_2, such that

$$\rho_2 + \rho_1 = \partial_1 F(0,0) - \varepsilon,$$
$$\rho_2 - \rho_1 = (\partial_2 F(0,0) - \varepsilon)(B'(0) - \varepsilon),$$

note that $\Phi_*(\xi) \le \sigma$ for any $\xi \le 0$. Choose $\sigma = (\sigma_1, \sigma_2) \ll 0$ with $\sigma_1 < \min\{\delta_1, \delta_3, \frac{\delta_2}{B'(0)}\}$. It then follows from (2.5) that

$$\begin{aligned}
&c\phi_*'(\xi) + c\psi_*'(\xi) - D\phi_*''(\xi)\\
=&F(\phi_*(\xi), (G**B(\phi_*))(\xi))\\
\ge&(\partial_1 F(0,0) - \varepsilon)\phi_*(\xi) + (\partial_2 F(0,0) - \varepsilon)(G**B(\phi_*))(\xi)\\
\ge&(\partial_1 F(0,0) - \varepsilon)\phi_*(\xi) + (\partial_2 F(0,0) - \varepsilon)(B'(0) - \varepsilon)(G**\phi_*)(\xi)\\
=&(\rho_2 + \rho_1)\phi_*(\xi) + (\rho_2 - \rho_1)(G**\phi_*)(\xi)\\
=&\rho_1[\phi_*(\xi) - (G**\phi_*)(\xi)] + \rho_2[\phi_*(\xi) + (G*\phi_*)(\xi)],
\end{aligned} \tag{4.9}$$

integrating both sides of (4.9) from y to 0 with $y < 0$, we have

$$\begin{aligned}
&c[\phi_*(0) - \phi_*(y)] + c[\psi_*(0) - \psi_*(y)] - D[\phi_*'(0) - \phi_*'(y)] + \rho_1 \int_y^0 [(G**\phi_*)(\xi) - \phi_*(\xi)]d\xi\\
\ge&\rho_2 \int_y^0 [\phi_*(\xi) + (G**\phi_*)(\xi)]d\xi,
\end{aligned} \tag{4.10}$$

note that $\Phi_*(\xi) = T(\Phi_*)(\xi)$. Direct calculations show that

$$\begin{aligned}
\phi_*'(\xi) =&\frac{1}{D(r_2 - r_1)}\left[r_1 \int_{-\infty}^{\xi} e^{r_1(\xi-\hat{s})} S_1(\Phi_*)(\hat{s})d\hat{s} + r_2 \int_{\xi}^{+\infty} e^{r_2(\xi-\hat{s})} S_1(\Phi_*)(\hat{s})d\hat{s}\right],\\
\psi_*'(\xi) =& -\frac{\gamma_2}{c^2}\int_{-\infty}^{\xi} e^{-\frac{\gamma_2}{c}(\xi-\hat{s})} S_2(\Phi_*)(\hat{s})d\hat{s} + \frac{1}{c}S_2(\Phi_*)(\xi),
\end{aligned}$$

since $S(\Phi_*)$ is bounded, the above equalities imply that $\Phi_*'(\xi)$ is uniformly bounded in $\mathbb{R}$. By Fubini's Theorem, we have

$$\begin{aligned}
&\left|\int_y^0 [(G**\phi_*)(\xi) - \phi_*(\xi)]d\xi\right|\\
=&\left|\int_y^0 \left[\int_0^{+\infty}\int_{\mathbb{R}} G(x,s)\phi_*(\xi - x - cs)dxds - \phi_*(\xi)\right]d\xi\right|\\
=&\left|\int_y^0 \left[\int_0^{+\infty}\int_{\mathbb{R}} G(x,s)(x+cs)\int_0^1 \phi_*'(\xi - \theta(x+cs))d\theta dxds\right]d\xi\right|\\
=&\left|\int_0^{+\infty}\int_{\mathbb{R}} G(x,s)(x+cs)\int_0^1 [\phi_*(-\theta(x+cs)) - \phi_*(y - \theta(x+cs))]d\theta dxds\right|,
\end{aligned}$$

note that (C1) implies that $\int_0^{+\infty}\int_{\mathbb{R}} |x+cs|G(x,s)dxds < +\infty$. Hence, we have

$$\left|\int_y^0 [(G**\phi_*)(\xi) - \phi_*(\xi)]d\xi\right| \le 2K^+ \int_0^{+\infty}\int_{\mathbb{R}} |x+cs|G(x,s)dxds < +\infty,$$

this shows that $\int_y^0 [(G**\phi_*)(\xi) - \phi_*(\xi)]d\xi$ is bounded on $(-\infty, 0]$. Therefore, from (4.10), we see that $\int_y^0 \phi_*(\hat{s})d\hat{s}$ is bounded on $(-\infty, 0]$. Moreover, from the second equation of (2.5), we have

$$\gamma_2 \int_y^0 \psi_*(\hat{s})d\hat{s} = \gamma_1 \int_y^0 \phi_*(\hat{s})d\hat{s} - c[\psi_*(0) - \psi_*(y)],$$

which implies that $\int_y^0 \psi_*(\hat{s})d\hat{s}$ is also bounded on $(-\infty, 0]$. Hence, (4.8) follows.

By the uniform boundedness of Φ_*', we can show that $\Phi_*(-\infty) = \mathbf{0}$. The proof of upward convergence $\Phi_*(+\infty) = \mathbf{K}$ is essentially similar to that of Theorem 4.1 and thus omitted. □

5. Conclusion

The seed bank model (1.5), which incorporates dormancy, nonlocal reproduction, and spatio-temporal memory effects, provides a rich mathematical framework for investigating ecological invasion dynamics. Our analysis distinguishes two structurally distinct regimes *monotone* and *non-monotone* systems whose behaviors differ significantly with respect to traveling wave existence and invasion speed. In particular, the introduction of a *spatio-temporal delay* via the convolution term plays a pivotal role in shaping both the rate and spatial profile of biological spread.

Under the monotonicity condition (A5), the model admits monotone traveling wave solutions for all $c \geq c^*$, connecting the extinction state to the carrying capacity (Theorem 2.7). These results reflect idealized ecological scenarios where higher seed bank density or past reproductive effort strictly enhances active population growth. The system spreads in a smooth, predictable manner, and c^* quantifies the minimal rate at which such a front can advance (Theorem 2.3).

When the monotonicity condition (A5) is relaxed, the system becomes more ecologically realistic, capturing nonlinear feedbacks such as germination saturation, delayed activation, or recruitment thresholds. Even in this general case, our results confirm that c^* remains a valid threshold for invasion (Theorem 3.3). Although traveling waves may become non-monotone, they still exist for all $c > c^*$ (Theorem 4.1), while no such waves occur for $c < c^*$ (Theorem 3.4). These waves reflect more complex propagation patterns, such as overshoot or spatial layering, often observed in nature but beyond the reach of monotone models. Ecologically, the model shows that delayed and spatially distributed reproduction can slow the spreading speed c^* and generate non-monotonic invasion fronts, reflecting processes such as dormancy, delayed recruitment, and spatial heterogeneity that shape both the rate and pattern of range expansion.

Our current work has primarily focused on invasion dynamics and long-term convergence to the positive equilibrium $\mathbf{K}$. In future work, a natural extension is to examine whether the combined effects of spatio-temporal delay and non-monotonicity may destabilize the positive equilibrium $\mathbf{K}$. In the seed bank model (1.5), this type of instability can manifest as population oscillations, recurrent outbreaks, or spatial pattern formation, with important implications for species persistence, habitat colonization, and ecological resilience.

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