



Research article

A nonlocal population model for the invasion of Canada goldenrod*

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Abstract: A mathematical model for the population invasion of Canada goldenrod is proposed, with two reproductive modes, yearly periodic time delay and spatially nonlocal response caused by the influence of wind on the seeds. Under suitable conditions, we obtain the existence of the rightward and leftward invasion speeds and their coincidence with the minimal speeds of time periodic traveling waves. Furthermore, the invasion speeds are finite if the dispersal kernel of seeds is exponentially bounded and infinite if dispersal kernel is exponentially unbounded.

Keywords: Canada goldenrod; periodic delay; nonlocal dispersal; propagation dynamics

1. Introduction

Being introduced to Nanjing, Shanghai and other places in China since 1935, Canada goldenrod, as an ornamental flower, showed strong adaptability to the environment and related reports have appeared in many provinces in China [1]. It's able to survive in a wide range of environmental conditions and invade wasteland, river banks and newly planted forest land [2]. The huge number of seeds, lightly pappus and the nature that can spread with the wind, accelerates its spread effectively and efficiently [3]. As a clone plant, Canada goldenrod has a developed underground cloning system, which can produce a large number of clonal plants through underground stems and squeeze out the living space of native plants [2]. In places invaded by Canada goldenrod, the species diversity index of the plant community decreased with the expansion of it and the stability of the plant community was worse than that of areas without it. All these indicate that this species has greater ecological risk. Shen et al. [4] investigated the coverage of Canada goldenrod in some areas up to 100%, which caused great damage to species diversity. Therefore, it is meaningful to study the nature of the invasion of Canada goldenrod.

*In memory of Professor Stephen A. Gourley.

Canada goldenrod is perennial and has various organs of general plants and winter-dormant rhizomes [3]. During the invasion process, Canada goldenrod can first form multi-satellite populations through seed propagation, and then fill the gaps through underground stem clonal propagation, eventually forming a single dominant population to crowd out native plants. It was found in [5] that Canada goldenrod has the following growth characteristics.

(i) Under natural conditions, the germination season of Canada goldenrod lasts from March to October, with a germination peak in April and May. Vegetative growth was especially vigorous during the summer season. Most Canada goldenrod flower between September and January, and fruit in late October. After the seeds mature, the pedicels and the tops of the branches of the plant gradually dry and die;

(ii) Canada goldenrod reproduces asexually by underground rhizomes and nodes on the stem base to recruit new individuals, and uses this reproductive strategy to produce clonal shoots in plants that experience mechanical damage.

Based on these characteristics, one may see there are three periods in the whole life cycle: the seed period, the immature period and the mature period, as shown in Figure 1. In view of the perennial nature of Canada goldenrod, winter-dormant rhizomes underground can be regarded as the other kind of seed, which is asexual reproduction. In more detail, the population density of immaturity partly comes from seeds and rhizomes, produced by sexual and asexual reproduction, respectively. In this way, growth cycle for Canada goldenrod can be regarded as an annual cycle.

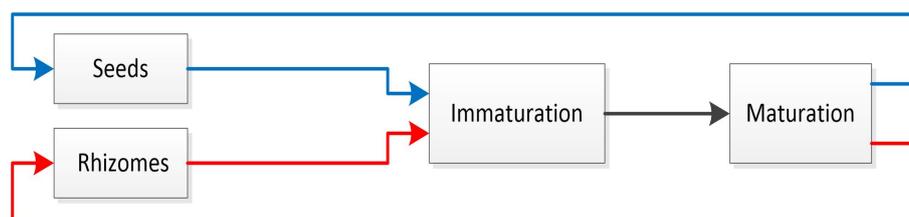


Figure 1. Schematic illustration of the life cycle for Canada goldenrod.

In this paper we make an attempt to use nonlocal and delayed differential equations to model the rapid invasion of Canada goldenrod. For this purpose, we first recall a partial list of related works by Stephen Gourley and his collaborators. In 1993, Gourley and Britton [6] studied a single-species population model where the animals are moving, leading to a nonlocal term in the nonlinearity. Al-Omari and Gourley [7] derived a partially coupled diffusive population model, in which the mature population is a delay differential equation. They proved the monotonicity of travelling fronts. Gourley and Kuang [8] formulated and studied a single-species diffusive delay population model. Gourley and Ruan [9] investigated a two-species competition model described by a reaction-diffusion system with nonlocal delays. For more related works on delayed nonlocal diffusive models, we refer to the survey articles [10–12] and references therein.

The nonlocal dispersal had been found to be appropriate to account for long distance moving, for example, cane toads [13], Reid's paradox of tree migration [14], the European green crab [15], as well as infectious individuals [16], and so on. Szymańska et al. [17] also focused on the role of nonlocal kinetic terms modelling competition for space and degradation with nonlocal terms describing the interactions between cancer cells and the host tissue. Garnier [18] studied the spreading properties of

the solutions of an integro-differential equation of the form

$$u_t = J * u - u + f(u).$$

He proved that for kernels $J(x)$, which decrease to 0 slower than any exponentially decaying function, the level sets of the solution u propagate with an infinite asymptotic speed. More recently, Pan et al. [19] studied the influence of seasonal successions on propagation of an age-structured invasive species by poincaré map, where delay is time periodic and there is no nonlocal diffusion. They found that time delay decreases the speed and its periodicity may further do so. Pan et al. [20] investigated the propagation of a system, defined by iterations of the Poincaré map of a population model with symmetric nonlocal dispersal and periodic time delay. They showed that the system admits the spreading speed $c^* \in (0, +\infty]$ that coincides with the minimal speed of traveling waves, where $c^* = +\infty$ if $J(x)$ is symmetrically decreasing and has a fat tail that is bigger than any exponential functions, which further gives rises to an accelerating propagation.

Why does the goldenrod spread so fast? From its lifecycle, we see that its seeds can spread by wind and its rhizomes can also expand locally. According to its biological performance, we may ideally divide its growth cycle into Seed dispersal, Rhizome expansion, Germinating season and Maturation season.

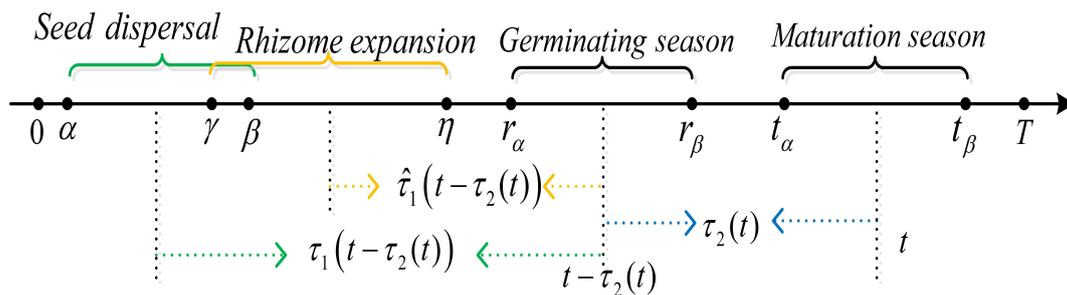


Figure 2. As the seasons change, there are different growth periods for Canada goldenrod in a year, where $[\alpha, \beta]$ is the nonlocal dispersal season of seeds, $[\gamma, \eta]$ is the local diffusion period of rhizomes, $[r_\alpha, r_\beta]$ is the germinating season, and $[t_\alpha, t_\beta]$ is the maturation season.

According to the biological characteristics of Canada goldenrod, we reasonably establish the following assumptions.

- (B1) $\tau_1(t)$ represents the duration from Seed dispersal to Germinating season, $\hat{\tau}_1(\cdot)$ represents the duration from Rhizome expansion to Germinating season and $\tau_2(\cdot)$ represents the duration from Germinating season to Maturation season, as shown in the Figure 2.
- (B2) Seeds and rhizomes germinate in the same germination season, as shown in Figure 2.
- (B3) An individual at time t belongs to the immature class if and only if its age exceeds 0 but does not exceed $\tau_2(t)$. An individual at time t belongs to the mature class if and only if its age exceeds $\tau_2(t)$.

Start from these biological assumptions, we will propose a nonlocal reaction-diffusion model, see (2.8) in the next section. In this model, two dispersal mechanisms are involved; one is the nonlocal dispersal that models the long distance flying of seeds with the help of winds, the other is the local dispersal that models the gradual spread of rhizomes under the ground. The established formula (5.4)

for leftward/rightward spreading speed implies that seeds and rhizomes have their unique contributions to the successful invasion; in particular, seeds can fly with a long distance (i.e., the dispersal kernel J has a fat tail), which can result in rapid and even accelerated invasion, see Theorem 5.2(ii). Also, from the formula (5.4) and the properties of \mathcal{K} (see (3.11) and (3.12) and Lemma 4.1), we may see that even without seeds the goldenrod still can spread by their rhizomes since \mathcal{K} consists of two parts; one part is due to seed dispersal, the other part is due to rhizome dispersal (see the expression (3.11) of \mathcal{K}). These findings may further suggest the following control strategy: to prevent rapid invasion of goldenrod one can choose to remove the aboveground inflorescence of goldenrod before the seeds are fully matured, and to stop the invasion of goldenrod one needs additionally to pull out and destroy the underground rhizomes.

The rest of this paper is organized as follows. Section 2 is devoted to derivation of model. In Section 3, we investigate the global dynamics for the corresponding spatially homogeneous system by the Poincaré map. Section 4 consists of several properties for kernel, in cases of exponential bounded and unbounded dispersal kernels, that will be essential for study of propagation properties. In Section 5, by appealing to the dynamical system theory we establish the existence of rightward/leftward spreading speeds and their characterizations. In Section 6, we go back to the original continuous system and establish propagation dynamics for the mature and immature growth stages of Canada goldenrod. Finally a short summary and discussion concludes the paper.

2. Derivation of model

Recall the following growth law for age-structured populations (e.g., [21]):

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right)\rho(t, a, x) = -d(t, a)\rho(t, a, x), \quad (2.1)$$

where $\rho(t, a, x)$ denotes the density of Canada goldenrod of age a at time t and location x , $d(t, a)$ is the death rate. Presently, we can define the density of species in different life period.

$$I(t, x) = \int_0^{\tau_2(t)} \rho(t, a, x) da, \quad M(t, x) = \int_{\tau_2(t)}^{+\infty} \rho(t, a, x) da.$$

$$d(t, a) = \begin{cases} d_I(t), & a \in (0, \tau_2(t)]; \\ d_M(t), & a \in (\tau_2(t), +\infty). \end{cases}$$

where $d_I(t)$ and $d_M(t)$ are the death rate of the immature and mature Canada goldenrod, respectively. From a biological point of view, the density of the species goes to zero when age tends to infinity, that is $\rho(t, +\infty, x) = 0$. Differentiating t in the above equations then yields

$$\begin{cases} \frac{\partial}{\partial t} I(t, x) = -d_I(t)I(t, x) + \rho(t, 0, x) - (1 - \tau_2'(t))\rho(t, \tau_2(t), x), \\ \frac{\partial}{\partial t} M(t, x) = -d_M(t)M(t, x) + (1 - \tau_2'(t))\rho(t, \tau_2(t), x). \end{cases} \quad (2.2)$$

Now we are in position to computing $\rho(t, 0, x)$ and $\rho(t, \tau_2(t), x)$ by employing an evolution viewpoint. A key step is to establish $\rho(t, 0, x)$, stemming from the evolution of seeds and rhizomes, as

illustrated in Figures 1 and 2. To do this, we introduce $u_1(r, x) = \tilde{\rho}_1(t - \tau_1(t) + r, r - \tau_1(t), x)$ with $r \in (0, \tau_1(t)]$ and $u_2(r, x) = \tilde{\rho}_2(t - \hat{\tau}_1(t) + r, r - \hat{\tau}_1(t), x)$ with $r \in (0, \hat{\tau}_1(t)]$ to represent the densities of seeds and rhizomes, respectively. Starting from the spread of seeds and rhizomes, we get the following evolution systems:

$$\begin{cases} \frac{\partial}{\partial r} u_1(r, x) = D_S(t - \tau_1(t) + r)(J * u_1 - u_1)(r, x) - d_S(t - \tau_1(t) + r)u_1(r, x), & r \in (0, \tau_1(t)], \\ u_1(0, x) = \tilde{\rho}_1(t - \tau_1(t), -\tau_1(t), x), \end{cases} \quad (2.3)$$

$$\begin{cases} \frac{\partial}{\partial r} u_2(r, x) = D_R(t - \hat{\tau}_1(t) + r) \frac{\partial^2 u_2(r, x)}{\partial x^2} - d_R(t - \hat{\tau}_1(t) + r)u_2(r, x), & r \in (0, \hat{\tau}_1(t)], \\ u_2(0, x) = \tilde{\rho}_2(t - \hat{\tau}_1(t), -\hat{\tau}_1(t), x), \end{cases} \quad (2.4)$$

where $D_S(t - \tau_1(t) + r)$ and $D_R(t - \hat{\tau}_1(t) + r)$ are the diffusive rate of seeds and rhizomes, respectively. $d_S(t - \tau_1(t) + r)$ and $d_R(t - \hat{\tau}_1(t) + r)$ are the death rate of seeds and rhizomes, respectively. In view of seeds are produced by mature individuals, $\tilde{\rho}_1(t - \tau_1(t), -\tau_1(t), x) = b_1(t - \tau_1(t), M(t - \tau_1(t), x))$, where b_1 is the birth function of seeds. Similarly, $\tilde{\rho}_2(t - \hat{\tau}_1(t), -\hat{\tau}_1(t), x) = b_2(t - \hat{\tau}_1(t), M(t - \hat{\tau}_1(t), x))$, where b_2 is the birth function of rhizomes. Write $K_S(t - \tau_1(t) + r, t - \tau_1(t), x)$ and $K_R(t - \hat{\tau}_1(t) + r, t - \hat{\tau}_1(t), x)$ as the Green functions of (2.3) and (2.4), respectively. Thus,

$$\begin{aligned} \rho(t, 0, x) &= K_S(t, t - \tau_1(t), \cdot) * b_1(t - \tau_1(t), M(t - \tau_1(t), \cdot))(x) \\ &\quad + K_R(t, t - \hat{\tau}_1(t), \cdot) * b_2(t - \hat{\tau}_1(t), M(t - \hat{\tau}_1(t), \cdot))(x). \end{aligned} \quad (2.5)$$

Next, we move forward to solve $\rho(t, \tau_2(t), x)$ by introducing $v(r, x) = \rho(t - \tau_2(t) + r, r, x)$ with $r \in (0, \tau_2(t)]$, we then see that $v(r, x)$ obeys the following laws by (2.1).

$$\begin{cases} \frac{\partial}{\partial r} v(r, x) = -d_I(t - \tau_2(t) + r)v(r, x), & r \in (0, \tau_2(t)], \\ v(0, x) = \rho(t - \tau_2(t), 0, x). \end{cases} \quad (2.6)$$

We first focus on $\rho(t - \tau_2(t), 0, x)$. As shown in Figures 1 and 2, immature individuals originate from the evolution of two parts: seeds and rhizomes. To simplify writing, we define

$$\tau(t) = \tau_2(t) + \tau_1(t - \tau_2(t)) \text{ and } \hat{\tau}(t) = \tau_2(t) + \hat{\tau}_1(t - \tau_2(t)). \quad (2.7)$$

It then follows from (2.5) that

$$\begin{aligned} \rho(t - \tau_2(t), 0, x) &= K_S(t - \tau_2(t), t - \tau(t), \cdot) * b_1(t - \tau(t), M(t - \tau(t), \cdot))(x) \\ &\quad + K_R(t - \tau_2(t), t - \hat{\tau}(t), \cdot) * b_2(t - \hat{\tau}(t), M(t - \hat{\tau}(t), \cdot))(x). \end{aligned}$$

Write $K_I(t - \tau_2(t) + r, t - \tau_2(t))$ as the Green function of (2.6). System (2.2) thus becomes

$$\left\{ \begin{array}{l} \frac{\partial}{\partial t} I(t, x) = -d_I(t)I(t, x) + K_S(t, t - \tau_1(t), \cdot) * b_1(t - \tau_1(t), M(t - \tau_1(t), \cdot))(x) \\ \quad + K_R(t, t - \hat{\tau}_1(t), \cdot) * b_2(t - \hat{\tau}_1(t), M(t - \hat{\tau}_1(t), \cdot))(x) \\ \quad - (1 - \tau'_2(t))K_I(t, t - \tau_2(t)) \\ \quad \cdot [K_S(t - \tau_2(t), t - \tau(t), \cdot) * b_1(t - \tau(t), M(t - \tau(t), \cdot))(x) \\ \quad + K_R(t - \tau_2(t), t - \hat{\tau}(t), \cdot) * b_2(t - \hat{\tau}(t), M(t - \hat{\tau}(t), \cdot))(x)], \\ \frac{\partial}{\partial t} M(t, x) = -d_M(t)M(t, x) + (1 - \tau'_2(t))K_I(t, t - \tau_2(t)) \\ \quad \cdot [K_S(t - \tau_2(t), t - \tau(t), \cdot) * b_1(t - \tau(t), M(t - \tau(t), \cdot))(x) \\ \quad + K_R(t - \tau_2(t), t - \hat{\tau}(t), \cdot) * b_2(t - \hat{\tau}(t), M(t - \hat{\tau}(t), \cdot))(x)], \end{array} \right. \quad (2.8)$$

Noticing that the equation of mature population is decoupled from the others, we first focus on the dynamics of mature equation. Define

$$\begin{aligned} & R_1(t, M(t - \tau(t), \cdot))(x) + R_2(t, M(t - \hat{\tau}(t), \cdot))(x) \\ & = (1 - \tau'_2(t))K_I(t, t - \tau_2(t))K_S(t - \tau_2(t), t - \tau(t), \cdot) * b_1(t - \tau(t), M(t - \tau(t), \cdot))(x) \\ & \quad + (1 - \tau'_2(t))K_I(t, t - \tau_2(t))K_R(t - \tau_2(t), t - \hat{\tau}(t), \cdot) * b_2(t - \hat{\tau}(t), M(t - \hat{\tau}(t), \cdot))(x). \end{aligned} \quad (2.9)$$

Then the solution map of mature population in (2.8) can be written as the following integral form

$$M(t, x) = K_M(t, 0)M(0, x) + \int_0^t K_M(t, l) [R_1(l, M(l - \tau(l), \cdot)) + R_2(l, M(l - \hat{\tau}(l), \cdot))](x) dl, \quad (2.10)$$

where $K_M(t, l) = e^{-\int_l^t d_M(\omega) d\omega}$.

According to (B1)–(B3) and the law of growth of Canada goldenrod, we further make the following reasonable assumptions mathematically:

- (A1) (Seasonality) $D_S > 0, D_R > 0, d_S > 0, d_R > 0, d_I > 0, d_M > 0, \tau_1 > 0, \tau_2 > 0, b_1 \geq 0, b_2 \geq 0, J \geq 0$ are all C^1 functions and T -periodic in time.
- (A2) (Distinct breeding, germinating and maturation seasons) Assume that $0 < \alpha, \gamma \leq \beta, \eta < r_\alpha \leq r_\beta < t_\alpha \leq t_\beta < T$, where t_α, t_β satisfy

$$t_\alpha - \tau_2(r_\alpha) = r_\alpha, \quad t_\beta - \tau_2(r_\beta) = r_\beta,$$

$$t_\alpha - \tau_2(t_\alpha) - \tau_1(t_\alpha - \tau_2(t_\alpha)) = \alpha, \quad t_\beta - \tau_2(t_\beta) - \tau_1(t_\beta - \tau_2(t_\beta)) = \beta,$$

$$t_\alpha - \tau_2(t_\alpha) - \hat{\tau}_1(t_\alpha - \tau_2(t_\alpha)) = \gamma, \quad t_\beta - \tau_2(t_\beta) - \hat{\tau}_1(t_\beta - \tau_2(t_\beta)) = \eta.$$

Further, we assume that $b_1(t, M) = p(t)h(M)$ and $b_2(t, M) = q(t)g(M)$, where $p \geq 0, q \geq 0, h \geq 0, g \geq 0$ and $p(t) \equiv 0$ for $t \in [0, \alpha] \cup [\beta, T]$. However, $q(t) \equiv 0$ for $t \in [0, \gamma] \cup [\eta, T]$.

- (A3) (Ordering in immaturation and maturation) $\tau'_1(t) < 1, \hat{\tau}'_1(t) < 1$ and $\tau'_2(t) < 1$.

(A4) (Unimodality of birth function) Assume that $h \in C^1, g \in C^1, h(0) = 0 = h(+\infty), g(0) = 0 = g(+\infty)$ and there exists z_1^* and z_2^* such that $h(z)$ is increasing for $z \in [0, z_1^*)$ and decreasing for $z \in [z_1^*, +\infty)$ and $g(z)$ is increasing for $z \in [0, z_2^*)$ and decreasing for $z \in [z_2^*, +\infty)$. Define $z^* := \min\{z_1^*, z_2^*\}$.

(A5) (Subhomogeneous) $h(\lambda z) \geq \lambda h(z)$ and $g(\lambda z) \geq \lambda g(z)$ for $z \geq 0$ and $\lambda \in (0, 1)$.

3. Dynamics of spatially homogeneous map

From an evolution viewpoint, the mature population experience only natural death, so the poincaré map of (2.10) during the year $[0, T]$ is

$$Q_T(\phi) = K_M(T, 0)\phi + \int_{t_\alpha}^{t_\beta} K_M(T, l) \cdot [R_1(l, K_M(l - \tau(l), 0)\phi) + R_2(l, K_M(l - \hat{\tau}(l), 0)\phi)](x)dl. \tag{3.1}$$

It is easy to see that Q_T maps $M((n - 1)T, x)$ to $M(nT, x)$ for $n \geq 1$.

Define the map $\bar{Q}_T : \mathbb{R} \rightarrow \mathbb{R}$ by

$$\bar{Q}_T[z] = zK_M(T, 0) + \int_{t_\alpha}^{t_\beta} K_M(T, l) \cdot [\bar{R}_1(l, zK_M(l - \tau(l), 0)) + \bar{R}_2(l, zK_M(l - \hat{\tau}(l), 0))]dl.$$

Define

$$L := \frac{K_M(T, 0)}{1 - K_M(T, 0)} \int_{t_\alpha}^{t_\beta} \frac{\partial_\phi \bar{R}_1(l, 0)}{K_M(l, l - \tau(l))} + \frac{\partial_\phi \bar{R}_2(l, 0)}{K_M(l, l - \hat{\tau}(l))} dl, \tag{3.2}$$

where

$$\begin{cases} \partial_\phi \bar{R}_1(t, 0) = \partial_\phi \tilde{R}_1(t, 0) \bar{K}_S(t - \tau_2(t), t - \tau(t)), \\ \partial_\phi \bar{R}_2(t, 0) = \partial_\phi \tilde{R}_2(t, 0) \bar{K}_R(t - \tau_2(t), t - \hat{\tau}(t)), \end{cases} \tag{3.3}$$

with

$$\partial_\phi \tilde{R}_1(t, 0) = (1 - \tau_2'(t))K_I(t, t - \tau_2(t))p(t - \tau(t))h'(0), \tag{3.4}$$

$$\partial_\phi \tilde{R}_2(t, 0) = (1 - \tau_2'(t))K_I(t, t - \tau_2(t))q(t - \hat{\tau}(t))g'(0). \tag{3.5}$$

and

$$\bar{K}_S(t, l) = \int_{\mathbb{R}} K_S(t, l, x)dx, \quad \bar{K}_R(t, l) = \int_{\mathbb{R}} K_R(t, l, x)dx. \tag{3.6}$$

Theorem 3.1. Assume that (A1)–(A5) hold. Then the following statements are valid:

(i) If $L > 1$, then \bar{Q}_T admits at least one positive fixed point. Denote the minimal one by M^* . Then $\lim_{n \rightarrow +\infty} \bar{Q}_T^n[z] = M^*$ provided that $z \in (0, M^*]$, $M^*K_M(\alpha, 0) \leq z^*$ and $M^*K_M(\gamma, 0) \leq z^*$, where z^* defined in (A4).

(ii) If $L < 1$, then $\lim_{n \rightarrow +\infty} \bar{Q}_T^n[z] = 0$ for $z > 0$.

Proof. (i) It is easy to see that

$$\lim_{z \rightarrow 0} \frac{\bar{R}_1(l, zK_M(l - \tau(l), 0))}{zK_M(l - \tau(l), 0)} = \partial_\phi \bar{R}_1(l, 0), \quad \text{uniformly in } l \in [0, T]. \tag{3.7}$$

$$\lim_{z \rightarrow 0} \frac{\bar{R}_2(l, zK_M(l - \hat{\tau}(l), 0))}{zK_M(l - \hat{\tau}(l), 0)} = \partial_\phi \bar{R}_2(l, 0), \quad \text{uniformly in } l \in [0, T]. \quad (3.8)$$

Note that

$$\begin{aligned} & \frac{1}{zK_M(T, 0)} (\bar{Q}_T[z] - z) \\ &= \frac{1}{zK_M(T, 0)} \left\{ K_M(T, 0)z - z + \int_{t_\alpha}^{t_\beta} K_M(T, l) [\bar{R}_1(l, zK_M(l - \tau(l), 0)) + \bar{R}_2(l, zK_M(l - \hat{\tau}(l), 0))] dl \right\} \\ &= 1 - \frac{1}{K_M(T, 0)} + \int_{t_\alpha}^{t_\beta} \frac{K_M(T, 0) \bar{R}_1(l, K_M(l - \tau(l), 0)z)}{zK_M(T, 0)K_M(l, l - \tau(l))K_M(l - \tau(l), 0)} dl \\ & \quad + \int_{t_\alpha}^{t_\beta} \frac{K_M(T, 0) \bar{R}_2(l, K_M(l - \hat{\tau}(l), 0)z)}{zK_M(T, 0)K_M(l, l - \hat{\tau}(l))K_M(l - \hat{\tau}(l), 0)} dl \\ & \rightarrow \begin{cases} \left[1 - \frac{1}{K_M(T, 0)}\right] (1 - L), & z \rightarrow 0, \\ 1 - \frac{1}{K_M(T, 0)} < 0, & z \rightarrow +\infty. \end{cases} \end{aligned} \quad (3.9)$$

If $L > 1$, then \bar{Q}_T admits at least one positive fixed point. Denote the minimal one by M^* . If, additionally, $M^*K_M(\alpha, 0) \leq z^*$ and $M^*K_M(\gamma, 0) \leq z^*$, then $\bar{Q}[z]$ is non-decreasing in $z \in [0, M^*]$, which implies that $\lim_{n \rightarrow +\infty} Q^n[z]$ exists, denoted by z_∞ . It is then easily to see that $z_\infty = M^*$.

(ii) From the calculation of (3.7) and (3.9) and the subhomogeneity of R_1 and R_2 , we infer that

$$\frac{\bar{Q}_T[z] - z}{zK_M(T, 0)} \leq \left[1 - \frac{1}{K_M(T, 0)}\right] (1 - L) < 0, \quad L < 1. \quad (3.10)$$

Naturally, there exists $\delta \in (0, 1)$ such that $\bar{Q}_T[z] \leq (1 - \delta)z$ for $z > 0$. Further, we get $\bar{Q}_T^n[z] \leq (1 - \delta)^n z$, which gives $\lim_{n \rightarrow +\infty} \bar{Q}_T^n[z] = 0$ for $z > 0$. The proof is complete. \square

Define

$$\mathcal{K}(y) := K_M(T, 0)\delta(y) + \int_{t_\alpha}^{t_\beta} K_M(T, l) [\partial_\phi R_1(l, 0)K_M(l - \tau(l), 0) + \partial_\phi R_2(l, 0)K_M(l - \hat{\tau}(l), 0)] dl, \quad (3.11)$$

where $\delta(y)$ is the Dirac measure and

$$\begin{cases} \partial_\phi R_1(t, 0) = \partial_\phi \tilde{R}_1(t, 0)K_S(t - \tau_2(t), t - \tau(t), x), \\ \partial_\phi R_2(t, 0) = \partial_\phi \tilde{R}_2(t, 0)K_R(t - \tau_2(t), t - \hat{\tau}(t), x), \end{cases} \quad (3.12)$$

with $\partial_\phi \tilde{R}_1(t, 0)$ and $\partial_\phi \tilde{R}_2(t, 0)$ defined in (3.4) and (3.5), respectively.

4. Properties of kernel \mathcal{K} defined in (3.11)

In what follows, we make the following Hypothesis:

Hypothesis (\mathcal{H}): $L > 1$, $M^*K_M(\alpha, 0) \leq z^*$ and $M^*K_M(\gamma, 0) \leq z^*$, where z^* is defined in (A4).

Hypothesis (\mathcal{J}): $J(x, t) > 0$ with $\int_{\mathbb{R}} J(x, t) dx = 1$, $J(x, t) = J(x, t + T)$ and J is nonincreasing in $|x|$ for every fixed $t \in \mathbb{R}$.

Hypothesis (\mathcal{J}) is consistent with the nature of seeds spreading with the wind. Recall that $\bar{K}_S(t, l)$ and $\bar{K}_R(t, l)$ are defined in (3.6).

Define

$$\left[\int_l^t D_S(l)J(l, x)dl \right]_{(n)} := \begin{cases} \underbrace{\left[\int_l^t D_S(l)J(l, x)dl \right] * \cdots * \left[\int_l^t D_S(l)J(l, x)dl \right]}_{n \text{ times}}, & n \geq 1; \\ \text{Dirac measure,} & n=0. \end{cases} \quad (4.1)$$

Lemma 4.1. Assume that Hypothesis (\mathcal{J}) is satisfied. Then \bar{K}_S and K_S have the following explicit expressions:

$$\bar{K}_S(t, l) = e^{-\int_l^t d_S(\zeta)d\zeta}, \quad (4.2)$$

$$K_S(t, l, x) = \bar{K}_S(t, l) e^{-\int_l^t d_S(\zeta)d\zeta} \left\{ \sum_{n=0}^{+\infty} \frac{\left[\int_l^t D_S(\xi)J(\xi, x)d\xi \right]_{(n)}}{n!} \right\}. \quad (4.3)$$

Proof. Recall that K_S is the Green function of $\partial_t \rho = D_S(t)(J * \rho - \rho) - d_S(t)\rho$. It follows that

$$\rho(t, x; l, \phi) = \int_{\mathbb{R}} K_S(t, l, x - y)\phi(y)dy, \quad t > l, x \in \mathbb{R}, \quad (4.4)$$

where $\rho(t, x; l, \phi)$ is the solution of ρ with initial value ϕ from time l to t . If $\phi \equiv 1$, then $\rho(t, x; l, \phi) = \int_{\mathbb{R}} K_S(t, l, y)dy$. Besides, $\rho(t, x; l, 1)$ satisfies $\partial_t \rho = -d_S(t)\rho$ with $\rho(l) = 1$, which means that $\rho(t, x; l, 1) = e^{-\int_l^t d_S(\xi)d\xi}$.

Next, we derive (4.3) and write the details of proof here. Let us consider the following iteration system.

$$\begin{cases} \partial_t \rho_{k+1}(t, x) = D_S(t)[J(\cdot, t) * \rho_k(t, \cdot)](x), \\ \rho_0(s, x) = \phi(x), \\ \rho_k(l, x) = \phi(x), \end{cases} \quad t > s \geq l \geq 0, k \geq 0, x \in \mathbb{R}. \quad (4.5)$$

By direct calculation, we obtain that

$$\rho_1(t, x) - \rho_1(l, x) = \left[\int_l^t D_S(\xi)J(\xi, \cdot)d\xi \right] * \phi(x) := F(t, \cdot) * \phi(x), \quad (4.6)$$

Then by differential properties of convolution, we have

$$\begin{aligned} & \rho_2(t, x) - \rho_2(l, x) \\ &= \int_l^t D_S(\xi)J(\xi, \cdot) * [F(\xi, \cdot) * \phi(x) + \rho_1(l, \cdot)]d\xi(x) \\ &= \left[\int_l^t F'_\xi(\xi, \cdot) * F(\xi, \cdot)d\xi \right] * \phi(x) + \left[\int_l^t D_S(\xi)J(\xi, \cdot)d\xi \right] * \rho_1(l, x) \\ &= \frac{F(t, \cdot) * F(t, \cdot) * \phi(x)}{2} + F(t, \cdot) * \phi(x). \end{aligned}$$

As such, by an induction argument, we conclude that

$$\rho_k(t, x; l, \phi) = \left\{ \sum_{n=0}^k \frac{\left[\int_l^t D_S(\xi)J(\xi, \cdot)d\xi \right]_{(n)}}{n!} \right\} * \phi(\cdot)(x), \quad \text{for } t > l \geq 0, x \in \mathbb{R}, k \geq 0. \quad (4.7)$$

By hypothesis (\mathcal{J}), there holds

$$\left[\int_l^t D_S(l)J(l, \cdot)dl \right]_{(n)} \leq \left[\int_l^t D_S(l)J(l, 0)dl \right] \left[\int_l^t D_S(l)dl \right]^{n-1}.$$

Then let $k \rightarrow +\infty$, it follows that for $x \in \mathbb{R}$,

$$\sum_{n=0}^{+\infty} \frac{[\int_l^t D_S(l)J(l, \cdot)dl]_{(n)}(x)}{n!} \leq \sum_{n=0}^{+\infty} \frac{\int_l^t D_S(l)J(l, 0)dl \left[\int_l^t D_S(l)dl \right]^{n-1}}{n!} = \frac{\int_l^t D_S(l)J(l, 0)dl}{\int_l^t D_S(l)dl} e^{\int_l^t D_S(l)dl}.$$

Applying the Weierstrass convergence theorem, we see that for any $t_0 > l$, the series $\sum_{n=0}^{+\infty} \frac{[\int_l^t D_S(l)J(l, \cdot)dl]_{(n)}(x)}{n!}$ convergence uniformly for all $x \in \mathbb{R}$ and $t \in [l, t_0]$. Consequently,

$$\rho(t, x; l, \phi) = e^{-\int_l^t d_S(\xi) + D_S(\xi)d\xi} \left\{ \sum_{n=0}^{+\infty} \frac{[\int_l^t D_S(l)J(l, \cdot)dl]_{(n)}(x)}{n!} \right\} * \phi. \quad (4.8)$$

The proof is complete. \square

Corollary 1. \bar{K}_R and K_R have the following explicit expressions:

$$\bar{K}_R(t, l) = e^{-\int_l^t d_R(\zeta)d\zeta}, \quad (4.9)$$

$$K_R(t, l, x) = \bar{K}_R(t, l) \frac{1}{\sqrt{4\pi \int_l^t D_R(s)ds}} e^{-\frac{x^2}{4 \int_l^t D_R(s)ds}}. \quad (4.10)$$

Note that $J(x, t)$ is asymmetric on x . Before presenting the properties of \mathcal{K} , we recall a definition on the decay rate of dispersal kernel $J(x, t)$.

Definition 4.2. (see e.g., [18]) We say $J(x, t)$ is exponentially bounded if there exists $\mu > 0$ such that $\int_{\mathbb{R}} J(x, t)e^{\mu|x|}dx < +\infty$ for every fixed $t \in \mathbb{R}$. We say $J(x, t)$ is exponentially unbounded if for any $\mu > 0$ there exists $x_\mu \in \mathbb{R}$ such that $J(x, t) \geq e^{-\mu|x|}$, $|x| \geq x_\mu$ for every fixed $t \in \mathbb{R}$.

Lemma 4.3. Assume that (A1)–(A5) and Hypotheses (\mathcal{H}) and (\mathcal{J}) are satisfied.. Then the following statements holds.

(i) \mathcal{K} is nonincreasing, continuous in $|x| \in \mathbb{R}^+ / 0$ and

$$\int_{\mathbb{R}} \mathcal{K}(y)dy \in (1, +\infty). \quad (4.11)$$

(ii) If $J(x, t)$ is exponential bounded, then for any $\mu \in (0, \mu_1^*)$ and $\mu \in (0, \mu_2^*)$,

$$\int_{\mathbb{R}} \mathcal{K}(y)e^{\mu y}dy < +\infty \text{ and } \int_{\mathbb{R}} \mathcal{K}(y)e^{-\mu y}dy < +\infty, \quad (4.12)$$

respectively, where μ_1^* and μ_2^* are defined as

$$\mu_1^* = \sup \left\{ \mu : \int_{\mathbb{R}} J(x, t) e^{\mu y} dy < +\infty \right\} \quad (4.13)$$

and

$$\mu_2^* = \sup \left\{ \mu : \int_{\mathbb{R}} J(x, t) e^{-\mu y} dy < +\infty \right\}. \quad (4.14)$$

(iii) If $J(x, t)$ is exponential unbounded, then

$$\int_{\mathbb{R}} \mathcal{K}(y) e^{\mu |y|} dy = +\infty. \quad (4.15)$$

Proof. (i) By (3.2), (3.3), (3.11), (3.12), (4.2) and Fubini's theorem, we get

$$\begin{aligned} \int_{\mathbb{R}} \mathcal{K}(y) dy &= K_M(T, 0) + \int_{\mathbb{R}} \int_{t_\alpha}^{t_\beta} K_M(T, l) \cdot [\partial_\phi R_1(l, 0) K_M(l - \tau(l), 0) + \partial_\phi R_2(l, 0) K_M(l - \hat{\tau}(l), 0)] dl dy \\ &= K_M(T, 0) + \int_{t_\alpha}^{t_\beta} K_M(T, l) [\partial_\phi \bar{R}_1(l, 0) K_M(l - \tau(l), 0) + \partial_\phi \bar{R}_2(l, 0) K_M(l - \hat{\tau}(l), 0)] dl \\ &= K_M(T, 0) + [1 - K_M(T, 0)] L \\ &= 1 + (L - 1)[1 - K_M(T, 0)]. \end{aligned}$$

Clearly, $K_M(T, 0) \in (0, 1)$, then $\int_{\mathbb{R}} \mathcal{K}(y) dy > 1$ due to $L > 1$, as previously assumed.

(ii) We use the comparison argument to prove this item. Let $I_{[-1,1]}$ be characteristic function on $[-1, 1]$. We consider the following evolution system.

$$\begin{cases} \rho_t = D_S(t)(J(t, \cdot) * \rho - \rho)(x) - d_S(t)\rho, t > l, x \in \mathbb{R}, \\ \rho(l, x) = I_{[-1,1]}(x). \end{cases} \quad (4.16)$$

From the proof of Lemma 3.1, we know that

$$\rho(t, x) = \int_{\mathbb{R}} K_S(t, l, x - y) I_{[-1,1]}(y) dy = \int_{-1}^1 K_S(t, l, x - y) dy. \quad (4.17)$$

In view of the asymmetry of $J(x, t)$ on x and (4.1), there exists $\sigma(x) \in [-1, 1]$ such that

$$\rho(t, x) = \int_{-1}^1 K_S(t, l, x - y) dy \geq K_S(t, l, x + \sigma), x \in \mathbb{R}. \quad (4.18)$$

Now we consider the eigenvalue problem of (4.16). Looking for $w(t)e^{\lambda t - \mu x}$ solving $\bar{\rho}_t(x) = D_S(t)(J(t, \cdot) * \bar{\rho} - \bar{\rho})(x) - d_S(t)\bar{\rho}$, we deduce that

$$\frac{w'(t)}{w(t)} + \lambda = D_S(t) \left[\int_{\mathbb{R}} J(t, y) e^{\mu y} dy - 1 \right] - d_S(t), \quad (4.19)$$

which is well defined for $\mu \in (0, \mu_1^*)$. Choosing

$$\lambda = \frac{1}{T} \int_0^T D_S(\xi) \left[\int_{\mathbb{R}} J(\xi, y) e^{\mu y} dy - 1 \right] d\xi - \frac{1}{T} \int_0^T d_S(\xi) d\xi. \quad (4.20)$$

Then we can obtain a positive periodic function $w(t)$ by solving (4.19). Choosing $\zeta > 0$ such that $w(0)e^{-\mu(x-\zeta)} \geq I_{[-1,1]}(x)$. Applying comparison principle, we obtain that

$$\rho(t, x) \leq w(t) e^{\lambda t - \mu(x-\zeta)}.$$

Further,

$$K_S(t, l, x) \leq \rho(t, x - \sigma) \leq w(t) e^{\lambda t + \mu(\zeta+1) - \mu x} := c_1(t, \mu) e^{-\mu x}, \forall x \in \mathbb{R}.$$

It then follows from (3.11), (3.12) and (4.10) that there exists $c_2(t, \mu) > 0$ such that $\mathcal{K}(y) \leq c_2(t, \mu) e^{-\mu y}$ and thus $\int_{\mathbb{R}} \mathcal{K}(y) e^{\mu y} dy < +\infty$ for any $\mu \in (0, \mu_1^*)$, where μ_1^* is defined in (4.13). Similarly, $\int_{\mathbb{R}} \mathcal{K}(y) e^{-\mu y} dy < +\infty$ for any $\mu \in (0, \mu_2^*)$, where μ_2^* is defined in (4.14).

(iii) By (4.3) we get

$$K_S(t, l, x) \geq \bar{K}_S(t, l) e^{-\int_l^t D_S(\xi) d\xi} \int_l^t D_S(\xi) J(\xi, x) d\xi. \quad (4.21)$$

If for any $\mu > 0$ there exists $x_\mu \in \mathbb{R}$ such that $J(x, t) \geq e^{-\mu|x|}$, $|x| \geq x_\mu$ for every fixed $t \in \mathbb{R}$, it then follows that $\int_{\mathbb{R}} \mathcal{K}(y) e^{\mu|y|} dy = +\infty$. The proof is complete. \square

5. The property of Spreading speeds

5.1. Notations

Denote the space C by

$$C := \{\phi : \mathbb{R} \rightarrow \mathbb{R} \mid \phi \text{ is bounded and continuous}\}.$$

We equip C with the compact open topology, that is, a sequence $\phi_n \rightarrow \phi$ in C means that $\phi_n(x)$ converges to $\phi(x)$ uniformly for x in every compact set. Denote $C_r := \{\phi \in C : r \geq \phi \geq 0\}$ for all $r > 0$. Define the monotone function space

$$\mathcal{M} := \{\phi : \mathbb{R} \rightarrow \mathbb{R} \mid \phi(x) \geq \phi(y), x \leq y\}. \quad (5.1)$$

which is also endowed with the compact open topology. Also, we may define the ordering in \mathcal{M} . For $\phi, \psi \in \mathcal{M}$, we write $\phi \geq \psi$ if $\phi(x) - \psi(x) \geq 0$ for all $x \in \mathbb{R}$. Denote $\mathcal{M}_r := \{\phi \in \mathcal{M} : r \geq \phi \geq 0\}$ for $r > 0$. Finally, a subset U of C is bounded if $\sup_{u \in U} \|u\|$ is finite. For $u \in U$ and closed interval $I \subset \mathbb{R}$, define the function $u_I \in C(I, \mathbb{R})$ by $u_I(x) = u(x)$ for all $x \in I$. Given a bounded $U \subset C$, we use U_I to denote the set of $\{u_I : u \in U\}$. We use the Kuratowski measure to define the noncompactness of U_I which is naturally endowed with the uniform topology. The measure is defined as follows.

$$\alpha(U_I) := \inf\{r > 0 \mid U_I \text{ has a finite open cover with diameter being less than } r\}. \quad (5.2)$$

The set U_I is precompact if and only if $\alpha(U_I) = 0$.

For any $y \in \mathbb{R}$, we define a translation operator T_y on \mathcal{M} by

$$T_y[\phi](x) = \phi(x - y), \forall x \in \mathbb{R}. \quad (5.3)$$

5.2. Existence of spreading speed and its variation form

Lemma 5.1. Assume that (A1)–(A5) and Hypotheses (\mathcal{H}) and (\mathcal{J}) are satisfied. Let z^* be defined in (A4), M^* be defined in Theorem 3.1 and the initial value $M_0 \in C(\mathbb{R}, \mathbb{R})$ satisfies $0 \leq M_0(x) \leq M^*$. Then $Q : C_{M^*} \rightarrow C_{M^*}$ has the following six properties:

- (i) $T_y Q = Q T_y, \forall y \in \mathbb{R}$;
- (ii) Q is continuous with respect to compact open topology;
- (iii) Q is order preserved in the sense that $Q[u] \geq Q[v]$ whenever $u \geq v$ in C_{M^*} ;
- (iv) $\bar{Q} : [0, M^*] \rightarrow [0, M^*]$ admits two fixed points 0 and M^* , and for any $\gamma \in (0, M^*)$ one has $Q[\gamma] > \gamma$;
- (v) $\alpha(Q[S])(0) = \alpha(S(0)) = 0$ for any $S \in C_{M^*}$;
- (vi) $Q[\lambda\phi] \geq \lambda Q[\phi], \phi \in C_{M^*}, \lambda \in (0, 1)$.

Proof. Item (i) is obvious. Item (iii) follows from the monotonicity of h on $[0, M^*]$. Item (iv) follows from Theorem 3.1. Item (v) follows from the boundedness of C_{M^*} . Item (vi) follows from (A5) and it then remains to check item (ii), that is, $Q_T[\phi_n] \rightarrow Q_T[\phi]$ as $\phi_n \rightarrow \phi$ in C_{M^*} . In virtue of (A5), we have

$$|R_1(l, K_M(l - \tau(l), 0)\phi_n) - R_1(l, K_M(l - \tau(l), 0)\phi)| \leq f_\xi(l)\partial_\phi R_1(l, 0) * |\phi_n - \phi|K_M(l - \tau(l), 0)$$

and

$$|R_2(l, K_M(l - \hat{\tau}(l), 0)\phi_n) - R_2(l, K_M(l - \hat{\tau}(l), 0)\phi)| \leq g_\xi(l)\partial_\phi R_2(l, 0) * |\phi_n - \phi|K_M(l - \hat{\tau}(l), 0),$$

where $\partial_\phi R_1(l, 0)$ and $\partial_\phi R_2(l, 0)$ are defined in (3.12). Then by the definition of Q_T in (3.1), (3.11) and the Fubini's theorem, we have

$$\begin{aligned} & |Q_T[\phi_n] - Q_T[\phi]| \\ & \leq K_M(T, 0)|\phi_n - \phi| + \int_{t_\alpha}^{t_\beta} K_M(T, l)|R_1(l, K_M(l - \tau(l), 0)\phi_n) - R_1(l, K_M(l - \tau(l), 0)\phi)|dl \\ & \quad + \int_{t_\alpha}^{t_\beta} K_M(T, l)|R_2(l, K_M(l - \hat{\tau}(l), 0)\phi_n) - R_2(l, K_M(l - \hat{\tau}(l), 0)\phi)|dl \\ & \leq K_M(T, 0)|\phi_n - \phi| + \int_{t_\alpha}^{t_\beta} K_M(T, l)f_\xi(l)\partial_\phi R_1(l, 0) * |\phi_n - \phi|K_M(l - \tau(l), 0)dl \\ & \quad + \int_{t_\alpha}^{t_\beta} K_M(T, l)g_\xi(l)\partial_\phi R_2(l, 0) * |\phi_n - \phi|K_M(l - \hat{\tau}(l), 0)dl \\ & \leq \int_{\mathbb{R}} \mathcal{K}(y)|\phi_n - \phi|(x - y)dy. \end{aligned}$$

Define $\psi_n := |\phi_n - \phi|$. We claim that if $\psi_n \rightarrow 0, \psi_n \in C_{M^*}$, then $\mathcal{K} * \psi_n \rightarrow 0$, that is, for any $\varepsilon > 0$ and $l > 0$, there exists $N = N(\varepsilon, l)$ such that $\mathcal{K} * \psi_n < \varepsilon$ for $|x| \leq l$ and $n \geq N$. Indeed, by (4.11), we know that for any $\varepsilon > 0$, there exists $c = c(\varepsilon)$ such that $\int_{|y| \geq c} \mathcal{K}(y) \leq \frac{\varepsilon}{2M^*}$. It then follows that

$$\begin{aligned} \mathcal{K} * \psi_n(x) &= \int_{|y| \geq c} \mathcal{K}(y)\psi_n(x - y)dy + \int_{|y| \leq c} \mathcal{K}(y)\psi_n(x - y)dy \\ &\leq \frac{\varepsilon}{2} + \int_{|y| \leq c} \mathcal{K}(y)\psi_n(x - y)dy. \end{aligned}$$

For any $l > 0$, $|x| \leq l$ and $|y| \leq c$ imply that $|x - y| \leq l + c$. For such $l + c$ and ε , since $\psi_n \rightarrow 0$, we see that there exists $N(\varepsilon, l) > 0$ such that

$$\psi_n(s) < \frac{\varepsilon}{2 \int_{\mathbb{R}} \mathcal{K}(y) dy}, |s| \leq l + c, n \geq N.$$

Therefore, $\mathcal{K} * \psi_n \leq \varepsilon$ for $|x| \leq l$ and $n \geq N$. The proof is complete. \square

In virtue of Lemma 5.1, Q_T is an operator on C_{M^*} satisfying item (i)–(vi) and let c^* be its asymptotic speed of spread. It is worth noting that $J(x, t)$ is asymmetric on x , which implies that the rightward direction of spreading is not equal to the leftward one. Define c_+^* and c_-^* respectively, where c_+^* represents the rightward spreading speed. Similarly, c_-^* defines the leftward spreading speed by choosing a nondecreasing initial function ϕ in the phase space

$$\{\phi : \mathbb{R} \rightarrow [0, M^*] \mid \phi(x) \leq \phi(y), x \leq y\},$$

whose monotonicity is opposite to that of (5.1). Based on Lemma 4.3, the conclusions about spreading speed are presented as follows.

Theorem 5.2. *Assume that (A1)–(A5) and Hypotheses (\mathcal{H}) and (\mathcal{J}) are satisfied. Then Poincaré map (3.1) admits leftward and rightward spreading speeds satisfying $c_-^* + c_+^* > 0$. Furthermore,*

- (i) $c_+^* < +\infty$ and $c_-^* < +\infty$ if $J(x, t)$ is exponentially bounded, and they can be characterized by the variational forms

$$c_+^* = \inf_{\mu \in (0, \mu_1^*)} \frac{1}{\mu} \ln \left\{ \int_{\mathbb{R}} e^{\mu y} \mathcal{K}(y) dy \right\}, \quad c_-^* = \inf_{\mu \in (0, \mu_2^*)} \frac{1}{\mu} \ln \left\{ \int_{\mathbb{R}} e^{-\mu y} \mathcal{K}(y) dy \right\}, \quad (5.4)$$

where μ_1^* , μ_2^* and $\mathcal{K}(y)$ are defined in (4.13), (4.14) and (3.11), respectively.

- (ii) $c_+^* = +\infty$ and $c_-^* = +\infty$ if $J(x, t)$ is exponentially unbounded.

Proof. According to Lemma 5.1, we have the existence of the rightward spreading speed c_+^* and the leftward one c_-^* in sense of [22, Theorem 2.17]. We first claim that $c_+^* + c_-^* > 0$. Let us postpone the proof of the claim and quickly reach the conclusion.

Recall that the poincaré map Q_T of (2.10) during $[0, T]$ is defined in (3.1), where $R_1 + R_2$ is defined in (2.9). Let L_T be the poincare map of

$$\frac{\partial}{\partial t} M(t, x) = -d_M(t)M(t, x) + \partial_\phi R_1(t, 0) * M(t - \tau(t), x) + \partial_\phi R_2(t, 0) * M(t - \hat{\tau}(t), x), \quad (5.5)$$

where $\partial_\phi R_1(t, 0)$ and $\partial_\phi R_2(t, 0)$ are defined in (3.12). As a result of (A5), we know that Q_T is sublinear. Then $Q_T[\phi] \leq L_T[\phi]$ for all $\phi \in C_{M^*}$. By (A2) and (A4), it is easily to check that for every $\varsigma \in (0, 1)$, there is a positive number ε such that $Q_T[\phi] \geq (1 - \varsigma)L_T[\phi]$ for all $\phi \in C_\varepsilon$. Accordingly, the corollary on page 371 of [23] tells us that if $\int_{\mathbb{R}} e^{\mu y} m(y; dy)$ converges for all μ , then the rightward spreading speed c_+^* can be characterized in the following manner.

$$c_+^* = \inf_{\mu > 0} (1/\mu) \ln \left\{ \int_{\mathbb{R}} e^{\mu y} m(y; dy) \right\}. \quad (5.6)$$

It is easily checked that

$$\int_{\mathbb{R}} e^{\mu y} m(y; dy) = \int_{\mathbb{R}} e^{\mu y} \mathcal{K}(y) dy,$$

where \mathcal{K} is defined in (3.11). Further, [24, Theorem 2.1] says that the formula (5.6) is valid, with the infimum taken only over the μ for which the integral converges, provided that $\int_{\mathbb{R}} e^{\mu y} m(y; dy)$ converges for at least one positive value of μ . Thus, by Lemma 4.3 we infer that $c_+^* < +\infty$ and $c_-^* < +\infty$ for $\mu \in (0, \mu^*)$, which can be characterized by (5.4).

Furthermore, in the light of [24, Theorem 2.2], combining with Lemma 4.3, we conclude that (ii) holds.

Proof of the claim. Let $A > 0$ and define

$$K_S^A(t, s, x) = \begin{cases} K_S(t, s, x), & -A \leq x \leq A, \\ 0, & \text{otherwise,} \end{cases}$$

In the form of $Q_T[\phi]$, we replace K_S by K_S^A , yielding an auxiliary map Q_T^A . Let $\mathcal{K}(y)$ be replaced by $\mathcal{K}^A(y)$. Then Q_T^A trivially admits leftward/rightward spreading speeds $c_{\pm}^*(A)$. Furthermore, it follows from [23, Proposition 5.5] that $c_+^* + c_-^* > c_+^*(A) + c_-^*(A)$, where $A > 0$ is sufficiently large to ensure that item (iv) in Lemma 5.1 holds, as well as item (i) in Lemma 4.3, that is

$$\int_{\mathbb{R}} \mathcal{K}^A(y) dy \in (1, +\infty). \quad (5.7)$$

Define

$$\lambda^A(\mu) = \frac{1}{T} \ln \left\{ \int_{\mathbb{R}} e^{\mu y} \mathcal{K}^A(y) dy \right\}, \quad (5.8)$$

where T is the period of system (2.8). In virtue of (3.1), (2.9) and the expression of K_R , that is

$$K_R(t, l, x) = \bar{K}_R(t, l) \frac{1}{\sqrt{4\pi \int_l^t D_R(s) ds}} e^{-\frac{x^2}{4 \int_l^t D_R(s) ds}},$$

we infer that

$$\lim_{\mu \rightarrow +\infty} \frac{1}{\mu} \lambda^A(\mu) = +\infty, \quad \lim_{\mu \rightarrow +\infty} \frac{1}{\mu} \lambda^A(-\mu) = +\infty.$$

Suppose that the minimum values of $\frac{\lambda(\pm\mu)}{\mu}$ are attained at $\mu_1 > 0$ and $\mu_2 > 0$ respectively, then by the convexity of the principle eigenvalue (See Ref. [22]), we have that

$$c_+^*(A) + c_-^*(A) \geq \frac{\mu_1 + \mu_2}{\mu_1 \mu_2} \lambda^A(0).$$

It then follows from (5.7) and (5.8) that the proof is complete. \square

6. Propagation dynamics of model (2.8) when $J(x, t)$ is exponentially bounded

Now we know the existence of spreading speeds and their variation expression. Further, we will describe the coincidence of spreading speeds with the minimal wave speed by discussing the existence of traveling waves. Besides, for the original model (2.8), the asymptotic property of periodic semiflow is shown, as well as the existence of periodic traveling wave.

6.1. The mature equation

Lemma 6.1. *Assume that the conditions in Lemma 5.1 hold. Then the conclusions in Lemma 5.1 still hold for Q_T with C_{M^*} being replaced by \mathcal{M}_{M^*} . Further, Q_T maps left-continuous or right-continuous functions to left-continuous or right-continuous functions, respectively.*

Proof. It suffices to prove that $Q_T : \mathcal{M}_{M^*} \rightarrow \mathcal{M}_{M^*}$ maps left-continuous functions to left-continuous functions because the conclusions in Lemma 5.1 are still valid with C_{M^*} being replaced by \mathcal{M}_{M^*} , which can be checked similarly with the proof of Lemma 5.1. Recall that

$$K_S(t, l, x) = \bar{K}_S(t, l) e^{-\int_l^t D_S(\xi) d\xi} \sum_{n=0}^{+\infty} \frac{[\int_l^t D_S(l) J(l, \cdot) dl]_{(n)}}{n!}(x), t > l \geq 0. \quad (6.1)$$

Note that $\sum_{n=0}^{+\infty} \frac{1}{n!} [\int_l^t D_S(l) J(l, \cdot) dl]_{(n)} \in L^1$ in view of hypothesis (\mathcal{J}). Applying the Lebesgue dominated convergence theorem, we know that $K_S(t, l, \cdot) * \phi$ is left-continuous if ϕ is left-continuous, so is $K_R(t, l, \cdot) * \phi$. In view of (2.9) and (3.1), we know that Q_T maps left-continuous or right-continuous functions to left-continuous or right-continuous functions, respectively. \square

Applying the dynamical system theory in [25], we shall establish the existence of the minimal wave speed and its coincide with c_+^*/T , as well as the existence of T -periodic traveling wave.

Lemma 6.2. $\{Q_t\}_{t \geq 0}$ is T -periodic semiflow on C_{M^*} with Q_T being defined in (3.1).

Proof. It is worth noting that $\{Q_t\}_{t \geq 0}$ has an explicit expression for $t \in [0, T]$, in view of (2.10) and the mature population experience only natural death. Obviously, $Q_0[v] = v, \forall v \in C_{M^*}$. It follows from a standard argument that $Q(t, v) := Q_t[v]$ is continuous in (t, v) on $[0, +\infty) \times C_{M^*}$. Finally, as a special case of [26, Lemma 3.5], it is easy to check that $Q_{t+T}[v] = Q_t[Q_T[v]], \forall t \geq 0, v \in C_{M^*}$, which completes the proof. \square

Let $W_1(t, x - ct)$ be a periodic traveling wave of the T -periodic semiflow $\{Q_t\}_{t \geq 0}$. We say that $W_1(t, x - ct)$ connects $M^*(t)$ to 0 if $W_1(t, -\infty) = M^*(t)$ and $W_1(t, +\infty) = 0$. In view of Lemma 6.1, 6.2 and [25, Remark 3.7, Theorem 3.8], we obtain the following conclusions:

Theorem 6.3. *Assume that (A1)–(A5) and Hypotheses (\mathcal{H}) and (\mathcal{J}) are satisfied. Suppose that $J(x, t)$ is exponentially bounded, that $M^* = M^*(0)$ and that c_+^* and c_-^* are the rightward and leftward asymptotic spread speeds of Q_T respectively, satisfying $c_-^* + c_+^* > 0$. Then following statements are valid:*

(i) *For any $c > c_+^*/T$ and $c' > c_-^*/T$, if $v \in C_{M^*}$ with $0 \leq v \leq M^*$, and $v(0, x) = 0$ for x outside a bounded interval, then*

$$\lim_{t \rightarrow +\infty, x \geq ct \text{ or } x \leq -c't} Q_t[v](x) = 0;$$

(ii) *For any $-c_-^*/T < -c' < c < c_+^*/T$ and $\sigma >> 0$, if $v \in C_{M^*}$ and $v(0, x) \geq \sigma$ for x on any interval of length $l > 0$, then*

$$\lim_{t \rightarrow +\infty, -c't \leq x \leq ct} |Q_t[v](x) - M^*(t)| = 0; \quad (6.2)$$

(iii) *For every $c < c_+^*/T$, $\{Q_t\}_{t \geq 0}$ admits no T -periodic traveling wave $W_1(t, x - ct)$ connecting $M^*(t)$ to 0, and for every $c > c_+^*/T$, $\{Q_t\}_{t \geq 0}$ has a T -periodic traveling wave $W_1(t, x - ct)$ connecting $M^*(t)$ to 0 such that $W_1(t, s)$ is left-continuous and nonincreasing in $s \in \mathbb{R}$;*

(iv) For any $c < c^*/T$, $\{Q_t\}_{t \geq 0}$ admits no T -periodic traveling wave $W_2(t, x + ct)$ connecting 0 to $M^*(t)$, and for any $c > c^*/T$, $\{Q_t\}_{t \geq 0}$ has a T -periodic traveling wave $W_2(t, x + ct)$ connecting 0 to $M^*(t)$ such that $W_2(t, s)$ is right-continuous and nondecreasing in $s \in \mathbb{R}$.

6.2. The immature equation

Write the immature equation in (2.8) briefly as

$$\begin{aligned} \frac{\partial}{\partial t} I(t, x) = & -d_I(t)I(t, x) + F_1(t, M(t - \tau_1(t), \cdot))(x) + F_2(t, M(t - \hat{\tau}_1(t), \cdot))(x) \\ & - R_1(t, M(t - \tau(t), \cdot))(x) - R_2(t, M(t - \hat{\tau}(t), \cdot))(x), \end{aligned} \quad (6.3)$$

where $R_1 + R_2$ is defined in (2.9) and

$$F_1(t, M(t - \tau_1(t), \cdot))(x) = K_S(t, t - \tau_1(t), \cdot) * b_1(t - \tau_1(t), M(t - \tau_1(t), \cdot))(x), \quad (6.4)$$

$$F_2(t, M(t - \hat{\tau}_1(t), \cdot))(x) = K_R(t, t - \hat{\tau}_1(t), \cdot) * b_2(t - \hat{\tau}_1(t), M(t - \hat{\tau}_1(t), \cdot))(x). \quad (6.5)$$

We have used the evolution idea introduced in [25] to show that c^*/T is the spreading speed and the minimal speed of time periodic traveling waves for the mature population. Next we will use the conservation equality (see, e.g., [19]), to prove the same propagation dynamics of the immature population as the mature.

We first prove a conservation equality whose biological meaning is immature population will become mature in the same year as when they were born.

Lemma 6.4. Assume that (A1)–(A5) are satisfied. Let $M(t, x)$ be a solution of the mature equation in (2.8). Then

$$\begin{aligned} & \int_0^T K_I(t, l) \left(F_1(l, M(l - \tau_1(l), \cdot))(x) + F_2(l, M(l - \hat{\tau}_1(l), \cdot))(x) \right) dl \\ &= \int_0^T K_I(t, l) \left(R_1(l, M(l - \tau(l), \cdot))(x) + R_2(l, M(l - \hat{\tau}(l), \cdot))(x) \right) dl, \end{aligned} \quad (6.6)$$

where $K_I(t, l)$ is the Green function of $\partial_t \rho = -d_I(t)\rho$.

Proof. From the definition of $R_1 + R_2$ in (2.9), and combining with the group property of K_I , we have

$$\begin{aligned} & K_I(t, l) \left(R_1(l, M(l - \tau(l), \cdot))(x) + R_2(l, M(l - \hat{\tau}(l), \cdot))(x) \right) \\ &= (1 - \tau'_2(l)) K_I(t, l - \tau_2(l)) \\ & \quad \cdot \left[K_S(l - \tau_2(l), l - \tau(l), \cdot) * b_1(l - \tau(l), M(l - \tau(l), \cdot))(x) \right. \\ & \quad \left. + K_R(l - \tau_2(l), l - \hat{\tau}(l), \cdot) * b_2(l - \hat{\tau}(l), M(l - \hat{\tau}(l), \cdot))(x) \right]. \end{aligned} \quad (6.7)$$

Note that for $l \notin [t_\alpha, t_\beta]$, $R_1(l, \phi) \equiv 0$ and $R_2(l, \phi) \equiv 0$. Similarly, for $l \notin [r_\alpha, r_\beta]$, $F_1(l, \psi) \equiv 0$ and $F_2(l, \psi) \equiv 0$. Besides, $b_1(l, \phi) \equiv 0$ for $l \notin [\alpha, \beta]$, as well as $b_2(l, \phi) \equiv 0$ for $l \notin [\gamma, \eta]$. It then follows

from (6.7) and (2.7) that

$$\begin{aligned}
 & \int_0^T K_I(t, l) \left(R_1(l, M(l - \tau(l), \cdot))(x) + R_2(l, M(l - \hat{\tau}(l), \cdot))(x) \right) dl \\
 = & \int_{t_\alpha}^{t_\beta} K_I(t, l) \left(R_1(l, M(l - \tau(l), \cdot))(x) + R_2(l, M(l - \hat{\tau}(l), \cdot))(x) \right) dl \\
 = & \int_{r_\alpha}^{r_\beta} K_I(t, s) K_S(s, s - \tau_1(s), \cdot) * b_1(s - \tau_1(s), M(s - \tau_1(s), \cdot))(x) ds \\
 & + \int_{r_\alpha}^{r_\beta} K_I(t, s) K_R(s, s - \hat{\tau}_1(s), \cdot) * b_2(s - \hat{\tau}_1(s), M(s - \hat{\tau}_1(s), \cdot))(x) ds \\
 = & \int_0^T K_I(t, s) \left(F_1(s, M(s - \tau_1(s), \cdot))(x) + F_2(s, M(s - \hat{\tau}_1(s), \cdot))(x) \right) ds.
 \end{aligned}$$

The proof is complete. \square

Clearly, the immature equation is linear and inhomogeneous in (6.3). Then we write it as the following integral form

$$I(t, x) = K_I(t, 0)I(0, x) + \int_0^t K_I(t, l)Y(l, x)dl, \quad (6.8)$$

where

$$\begin{aligned}
 Y(l, x) := & F_1(l, M(l - \tau_1(l), \cdot))(x) + F_2(l, M(l - \hat{\tau}_1(l), \cdot))(x) \\
 & - R_1(l, M(l - \tau(l), \cdot))(x) - R_2(l, M(l - \hat{\tau}(l), \cdot))(x).
 \end{aligned} \quad (6.9)$$

Now we are in position to present the propagation dynamics of the immature population.

Theorem 6.5. *Assume that (A1)–(A5) and Hypotheses (\mathcal{H}) and (\mathcal{J}) are satisfied and that $J(x, t)$ is exponentially bounded. Let $M^*(t)$ be defined in (6.2) and $M(t, x)$ be a solution of the mature equation in (2.8). Then the following statements are valid:*

- (i) *If $M(t, x) \equiv M^*(t)$, then (6.3) admits the unique nontrivial bounded periodic solution, defined as $I^*(t)$;*
- (ii) *If $M(t, x) = W_1(t, x - ct)$ is a periodic traveling wave, then (6.3) admits a unique periodic traveling wave $V_1(t, x - ct)$ with $V_1(t, +\infty) = 0$ and $V_1(t, -\infty) = I^*(t)$;*
- (iii) *If $M(t, x) = W_2(t, x + ct)$ is a periodic traveling wave, then (6.3) admits a unique periodic traveling wave $V_2(t, x + ct)$ with $V_2(t, -\infty) = 0$ and $V_2(t, +\infty) = I^*(t)$.*

Proof. In virtue of the proof of [19, Theorem 5.3], we first prove the uniqueness. We write down the details here. If there are two solutions $I_1(x, t)$ and $I_2(x, t)$, then $\tilde{I} := I_1 - I_2$ satisfies $\tilde{I}_t = -d_I(t)\tilde{I}(t, x)$, for which the only bounded solution is zero.

Next we prove the existence. Indeed, choosing $I(0, x) \equiv 0$, then (6.8) becomes

$$I(t, x) = \int_0^t K_I(t, l)Y(l, \cdot)(x)dl. \quad (6.10)$$

Now we proceed with two cases:

(i) $M(t, x) \equiv M^*(t)$. In this case, $Y(l, x)$ and $I(x, t)$ are respectively independent of x , written as $\bar{Y}(t)$ and $I^*(t)$. Clearly, $\bar{Y}(t)$ is periodic with $\int_0^T K_I(t, l)\bar{Y}(l)dl = 0$ in virtue of (6.6) and (6.9). Then

$$\begin{aligned} I^*(t+T) &= \int_0^{t+T} K_I(t+T, l)\bar{Y}(l)dl \\ &= \left[\int_0^T K_I(t, l)\bar{Y}(l)dl \right] K_I(t+T, t) + \int_T^{t+T} K_I(t+T, l)\bar{Y}(l)dl \\ &= \int_0^t K_I(t+T, r+T)\bar{Y}(r+T)d(r) \\ &= I^*(t). \end{aligned} \quad (6.11)$$

(ii) $M(t, x) = W_1(t, x - ct)$. Now

$$\begin{aligned} Y(l, x) &= F_1\left(l, W_1(l - \tau_1(l), \cdot - cl + c\tau_1(l))\right)(x) + F_2\left(l, W_1(l - \hat{\tau}_1(l), \cdot - cl + c\hat{\tau}_1(l))\right)(x) \\ &\quad - R_1\left(l, W_1(l - \tau(l), \cdot - cl + c\tau(l))\right)(x) - R_2\left(l, W_1(l - \hat{\tau}(l), \cdot - cl + c\hat{\tau}(l))\right)(x), \end{aligned}$$

and we define

$$V_1(t, \zeta) := \int_0^t K_I(t, l)Y(l, \cdot)(\zeta + ct)dl. \quad (6.12)$$

Obviously, $V_1(t, x - ct)$ is a solution of (6.3). Next we prove that V_1 is periodic in t . Indeed, note that $Y(l + T, x + cT) = Y(l, x)$ in the light of $W_1(t, x - ct)$ is a periodic traveling wave. It then follows from (6.8) that

$$\begin{aligned} V_1(t+T, \zeta) &= \int_T^{t+T} K_I(t+T, l)Y(l, \cdot)(\zeta + ct + cT)dl \\ &= \int_0^t K_I(t+T, \zeta + T)Y(\zeta + T, \cdot + cT)(\zeta + ct)d\zeta \\ &= V_1(t, \zeta). \end{aligned} \quad (6.13)$$

Finally, we prove $V_1(t, +\infty) = 0$ and $V_1(t, -\infty) = I^*(t)$. Indeed,

$$\begin{aligned} Y(l, +\infty) &= F_1\left(l, W_1(l - \tau_1(l), +\infty)\right)(x) + F_2\left(l, W_1(l - \hat{\tau}_1(l), +\infty)\right)(x) \\ &\quad - R_1\left(l, W_1(l - \tau(l), +\infty)\right)(x) - R_2\left(l, W_1(l - \hat{\tau}(l), +\infty)\right)(x), \end{aligned} \quad (6.14)$$

which is uniformly in $l \in \mathbb{R}$ in view of the periodicity in l . Furthermore, in (6.12), passing $\zeta \rightarrow +\infty$ we obtain that

$$V_1(t, +\infty) = \int_0^t K_I(t, l)Y(l, +\infty)dl. \quad (6.15)$$

Clearly, $V_1(t, +\infty) = 0$ and $V_1(t, -\infty) = I^*(t)$ by (6.14), (6.11) and Hypothesis (A4).

(iii) $M(t, x) = W_2(t, x + ct)$. After the similar discussion as case (ii), we can easily get that (6.3) admits the unique periodic traveling wave $V_2(t, x + ct)$ with $V_2(t, -\infty) = 0$, $V_2(t, +\infty) = I^*(t)$. Then the proof is complete. \square

Theorem 6.6. Assume that (A1)–(A5) and Hypotheses (\mathcal{H}) and (\mathcal{J}) are satisfied. Suppose that $J(x, t)$ is exponentially bounded and that $\phi \in C(\mathbb{R}, [0, M^*]) \setminus \{0\}$ and has a nonempty compact support. If $M(t, x; \phi)$ be a solution of the mature equation in (2.8) with rightward/leftward spreading speeds c_{\pm}^*/T , then, for any bounded initial condition $\psi, I(t, x; \psi)$ in (2.8) has the following property:

(i) For any $c > c_+^*/T$ and $c' > c_-^*/T$,

$$\limsup_{t \rightarrow +\infty, x \geq ct \text{ or } x \leq -c't} I(t, x; \psi) = 0; \tag{6.16}$$

(ii) For any $-c_-^*/T < -c' < c < c_+^*/T$,

$$\limsup_{t \rightarrow +\infty, -c't \leq x \leq ct} |I(t, x; \psi) - I^*(t)| = 0. \tag{6.17}$$

Proof. We first claim that for any fixed $(l, y) \in \mathbb{R}^+ \times \mathbb{R}$, the following statements are valid:

(1) For every $c > c_+^*/T$ and $c' > c_-^*/T$,

$$\limsup_{t \rightarrow +\infty, x \geq ct \text{ or } x \leq -c't} b_i(t - l, M(t - l, x - y)) = 0, i = 1, 2; \tag{6.18}$$

(2) For any $-c_-^*/T < -c' < c < c_+^*/T$,

$$\limsup_{t \rightarrow +\infty, -c't \leq x \leq ct} |b_i(t - l, M(t - l, x - y)) - b_i(t - l, M^*(t - l))| = 0, i = 1, 2. \tag{6.19}$$

Let us postpone the proof of the claim and reach the conclusion quickly. Define $N := \sup_{x \in \mathbb{R}} \|\psi(x)\|$. Define $s_1 = l + \tau_1(t - l)$, $\hat{s}_1 = l + \hat{\tau}_1(t - l)$, $s_2 = l + \tau_2(t - l)$, $s = l + \tau(t - l)$ and $\hat{s} = l + \hat{\tau}(t - l)$, $l \in [0, t]$. Then by (6.8) and (2.8), we infer that

$$\begin{aligned} I(t, x) \leq & NK_I(t, 0) + \int_0^t K_I(t, t - l) \int_{\mathbb{R}} K_S(t - l, t - s_1, y) \\ & \cdot b_1(t - s_1, M(t - s_1, x - y)) + K_R(t - l, t - \hat{s}_1, y) \\ & \cdot b_2(t - \hat{s}_1, M(t - \hat{s}_1, x - y)) dy - (1 - \tau_2'(t - l)) K_I(t - l, t - s_2) \\ & \cdot \int_{\mathbb{R}} [K_S(t - s_2, t - s, y) b_1(t - s, M(t - s, x - y)) \\ & + K_R(t - s_2, t - \hat{s}, y) b_2(t - \hat{s}, M(t - \hat{s}, x - y))] dy dl, \end{aligned}$$

where $K_I(t, 0) = e^{-\int_0^t d_l(\zeta) d\zeta}$. In advantage of the reverse Fatou’s lemma and (6.18), we infer that (6.16) holds. Using the same idea, we can prove that (6.17) holds, thanks to (6.19) and (6.11).

Proof of the claim. Thanks to (A4) and (A5),

$$b_1(t, M(t, x)) \leq p(t)h'(0)M(t, x)$$

and

$$b_2(t, M(t, x)) \leq q(t)g'(0)M(t, x).$$

Then by Theorem 6.3, we have

$$\limsup_{t \rightarrow +\infty, x \geq ct \text{ or } x \leq -c't} b_i(t, M(t, x)) = 0, i = 1, 2.$$

In virtue of the proof of [27, Theorem 3.2], (6.18) holds. Similarly, (6.19) holds thanks to Lipschitz continuity of $b_i(t, M(t, x)), i = 1, 2$. □

7. Conclusions

Based on the ecological characteristics of Canada goldenrod in literature, we ideally separate its life cycle into distinct stages and propose a toy stage-structured population model with two kinds of dispersal modes, see (2.8); trying to explain why the goldenrod can successfully invade with a fast speed. It turns out that the locally rhizome growth helps the goldenrod persist and the seed dispersal helps the goldenrod spread quickly.

More precisely, Theorem 3.1 establishes a threshold dynamics for the population persistence, where the threshold parameter L consists of two parts; one is increasing in the seed reproduction rate $p(t - \tau(t))h'(0)$ and the other is increasing in the rhizome growth rate. From this we can infer that a large turbulence on the seed reproduction (i.e., $p(t - \tau(t))$ might be small for some years) cannot significantly affect the persistence of Canada goldenrod, since the rhizome growth usually is more robust. However, seed can disperse with a long distance by wind, and hence it can result in fast invasion. By the variational characterization of the invasion speed established in Theorem 5.2, we see that the invasion speed heavily depends on the seed dispersal kernel J ; if J is exponentially bounded then the speed is finite, while if J is exponentially unbounded then the speed is infinite. The later case may result in an accelerating invasion, which will be studied in another work. When the invasion speed is finite, a family of time periodic invasion front are established in Theorem 6.3.

As a non-native plant, Canada goldenrod is now invading many places in East and Central China. For such an invasion phenomena, we found that few studies are done from mathematical modeling viewpoint. In field study, the invasion process is much more complicated than the ideal scenario that we assumed here. For example, the spatial heterogeneity is an important factor and it may cause various complexities. We hope this work may stimulate further studies for this plant invasion.

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Conflict of interest

The authors declare there is no conflict of interest.

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