Mathematical Biosciences and Engineering

http://www.aimspress.com/journal/MBE

MBE, 16(5): 4399–4414.
DOI: 10.3934/mbe.2019219
Received: 27 February 2018
Accepted: 24 April 2019
Published: 20 May 2019

Research article

Establishing *Wolbachia* in the wild mosquito population: The effects of wind and critical patch size

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Abstract: Releasing mosquitoes with *Wolbachia* into the wild mosquito population is becoming the very promising strategy to control mosquito-borne infections. To investigate the effects of wind and critical patch size on the *Wolbachia* establishment in the wild mosquito population, in this paper, we propose a diffusion-reaction-advection system in a heterogeneous environment. By studying the related eigenvalue problems, we derive various conditions under which *Wolbachia* can fully establish in the entire wild mosquito population. Our findings may provide some useful insights on designing practical releasing strategies to control the mosquito population.

Keywords: *Wolbachia*; advection; the minimal patch size; mosquito-borne; heterogeneous environment

1. Introduction

Mosquito-borne diseases such as malaria, dengue fever, West Nile virus, chikungunya, and Zika virus have been a great threat to public health. For dengue virus alone, it has been estimated that 3.9 billion people, in 128 countries, are at risk of infection [1]. In the year of 2014, more than 43,000 cases with locally acquired denguelike illness were reported in Guangdong province, China [2]. The human viruses including dengue, Zika, chikungunya and yellow fever are transmitted primarily by *Aedes aegypti* mosquitoes. Due to the lack of vaccines and efficient clinical cures [3], the only effective control strategy seems to be controlling the population of mosquitoes that transmit human viruses. Since massive spraying of insecticides and elimination of mosquito breeding sites are not sustainable to reduce mosquito density and might also lead to serious environmental problems, a promising strategy is the *Wolbachia* approach: releasing male and female *Aedes aegypti* mosquitoes with *Wolbachia* so that these mosquitoes can breed with the wild mosquito population and pass *Wolbachia* to the entire mosquito population. On one hand, the ability to transmit viruses to human for mosquitoes with *Wolbachia* is greatly reduced [4, 5]. On the other hand, since the *Wolbachia* infection often induces cytoplasmic incompatibility (CI), which leads to early embryonic death when *Wolbachia*-infected males mate with uninfected females [6, 7], the *Wolbachia* approach would greatly reduce the density of the mosquito population and can thus potentially eliminate the mosquito population and thus eradicate the mosquito-born infectious diseases.

To understand the *Wolbachia* infection dynamics, Zheng, Tang and Yu [8] proposed a delay differential equation model. To be self-contained, we briefly introduce their idea here. We denote by r_f and r_m the numbers of released female mosquitoes and released males carrying *Wolbachia*, respectively. Due to strong competition between adults, r_f and r_m satisfy

$$\begin{cases} \dfrac{\mathrm{d}r_f}{dt} = -\delta_1 r_f T(t), & t > 0, \\ \dfrac{\mathrm{d}r_m}{dt} = -\delta_1 r_m T(t), & t > 0. \end{cases} \tag{1.1}$$

Here $T(t) = r_f + r_m + I_f + I_m + U_f + U_m$ denotes the total population size, with U_f, U_m, I_f and I_m being the numbers of uninfected reproductive females, uninfected reproductive males, and infected reproductive females and males other than those from releasing, respectively. Let b_I (resp. b_U) be the natural birth rate of the infected (resp. uninfected) mosquitos and $0 \leq \delta \leq 1$ be the proportion of mosquitos born female. Then the proportion of mosquitos born male is $1 - \delta$. With strong CI and high maternal transmission, if the average waiting time from parent mating to the emergence of reproductive progenies for both infected and uninfected mosquitoes is negligible, then we have

$$\begin{cases} \dfrac{\mathrm{d}I_f}{dt} = \delta b_I[I_f + r_f] - \delta_1 I_f T(t), & t > 0, \\ \dfrac{\mathrm{d}I_m}{dt} = (1-\delta) b_I[I_f + r_m] - \delta_1 I_m T(t), & t > 0, \\ \dfrac{\mathrm{d}U_f}{dt} = \delta b_U \left[U_f \dfrac{U_m}{r_m + I_m + U_m}\right] - \delta_2 U_f T(t), & t > 0, \\ \dfrac{\mathrm{d}U_m}{dt} = (1-\delta) b_U \left[U_f \dfrac{U_m}{r_m + I_m + U_m}\right] - \delta_2 U_m T(t), & t > 0. \end{cases} \tag{1.2}$$

Since both r_f and r_m approach 0 as $t \to +\infty$. Let

$$u(t) = I_f + I_m \ \text{ and } \ v(t) = U_f + U_m. \tag{1.3}$$

Assuming equal determination case, which means that $\delta = 1/2$, $I_f = I_m$ and $U_f = U_m$, setting $b_1 = b_I/2$ and $b_2 = b_U/2$ and considering the spatiotemporal factor, Huang et al. [9] came up with the following reaction-diffusion system:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1\Delta u + u(b_1 - \delta_1(u+v)), & t>0, \quad x\in\Omega, \\ \dfrac{\partial v}{\partial t} = d_2\Delta v + v\left(\dfrac{b_2 v}{u+v} - \delta_2(u+v)\right), & t>0, \quad x\in\Omega, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & t>0, \quad x\in\partial\Omega, \\ u(0,x) = u_0(x), \quad v(0,x) = v_0(x), & x\in\Omega. \end{cases} \tag{1.4}$$

In (1.4), d_1 and d_2 are the diffusion rates, Δ denotes the Laplace operator in the spatial variable x, and ν denotes the unit outward normal vector to the boundary of Ω.

Noticing that the spread of mosquitoes can be greatly affected by the wind speed [10], therefore, the advection due to wind should be incorporated into modeling. Note also practical experience of releasing mosquitoes with *Wolbachia* to the wild suggests that a minimum release area is needed in order to achieve a stable local establishment and spread in continuous habitats [11]. Motivated by these two aspects, in this paper, we extend the model considered in [9], i.e., system (1.4), to a reaction-diffusion-advection model with spatially heterogeneous environment and flexible boundary conditions. More specifically, our model is described by the following system

$$\begin{cases} \dfrac{\partial u}{\partial t} = du_{xx} - \alpha u_x + u[b_1(x) - \delta_1(u+v)], & t>0, x\in(0,L), \\ \dfrac{\partial v}{\partial t} = dv_{xx} - \alpha v_x + v\left[\dfrac{b_2(x)v}{u+v} - \delta_2(u+v)\right], & t>0, x\in(0,L), \\ du_x(0,t) - \alpha u(0,t) = 0, & t>0, \\ du_x(L,t) - \alpha u(L,t) = -\beta\alpha u(L,t), & t>0, \\ dv_x(0,t) - \alpha v(0,t) = \beta\alpha v(0,t), & t>0, \\ dv_x(L,t) - \alpha v(L,t) = -\beta\alpha v(L,t), & t>0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x\in[0,L], \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x\in[0,L], \end{cases} \tag{1.5}$$

where $u(x,t)$ and $v(x,t)$ represent the population densities of infected and uninfected mosquitoes at location x and time t, respectively. The parameter d denotes the random diffusion rate of u and v. The functions $b_1(x)$ and $b_2(x)$ denote the halves of the birth rates of the infected and uninfected mosquitoes, respectively ([8]). The parameter δ_1 (or δ_2) denotes the density dependent death rate for the infected (or uninfected) mosquito species. The advection constant α measures the result of wind transportation. The parameter $\beta < \infty$ measures the relative rate of population loss at the downstream due to wind flow and replenishment at the upstream.

We suppose that $b_i(x)$ satisfies the following hypothesis:

$$b_i(x) \in C^{1+\alpha}([0,L])(\alpha\in(0,1)),\ i=1,2 \textit{ and } 0 < \underline{b} \leq b_1(x), b_2(x) \leq \bar{b}. \tag{1.6}$$

Here $\underline{b}$ and $\bar{b}$ are two positive constants.

We regard $\beta = +\infty$ as the Dirichlet boundary case, and system (1.5) becomes

$$\begin{cases} \dfrac{\partial u}{\partial t} = du_{xx} - \alpha u_x + u[b_1(x) - \delta_1(u+v)], & t > 0, x \in (0, L), \\ \dfrac{\partial v}{\partial t} = dv_{xx} - \alpha v_x + v\left[\dfrac{b_2(x)v}{u+v} - \delta_2(u+v)\right], & t > 0, x \in (0, L), \\ du_x(0,t) - \alpha u(0,t) = 0 = u(L,t), & t > 0, \\ v(0,t) = 0 = v(L,t), & t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x \in [0, L], \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in [0, L], \end{cases} \tag{1.7}$$

Ideally, if the entire mosquito population is replaced by mosquitoes with *Wolbachia*, then the *Wolbachia* establishment is called successful. This is achieved if the solutions of (1.5) and (1.7) approach a semi-trivial steady state, $(\widetilde{u}, 0)$, where $\widetilde{u}$ satisfies the following equations,

$$\begin{cases} du_{xx} - \alpha u_x + u[b_1(x) - \delta_1 u] = 0, & x \in (0, L), \\ du_x(0) - \alpha u(0) = 0, \\ du_x(L) - \alpha u(L) = -\beta\alpha u(L), \end{cases} \tag{1.8}$$

for $\beta < \infty$ or

$$\begin{cases} du_{xx} - \alpha u_x + u[b_1(x) - \delta_1 u] = 0, & x \in (0, L), \\ du_x(0) - \alpha u(0) = 0, \\ u(L) = 0, \end{cases} \tag{1.9}$$

for the case with $\beta = \infty$.

We point out that there has been several mathematical models formulated to describe the *Wolbachia* spreading dynamics. These models include differential equations with/without time delays [8, 12, 13, 14], reaction-diffusion equations [9, 15], and stochastic equations [16]. These models focused on studying the subtle relation between the threshold releasing level for *Wolbachia*-infected mosquitoes and several important parameters including the CI intensity and the fecundity cost of *Wolbachia* infection. We should also point out that besides releasing mosquitoes with *Wolbachia*, an alternative control strategy is releasing the sterile mosquitoes to the wild mosquito population [17].

We organize the rest of this paper as follows. In Section 2, we give some useful lemmas to establish the relation between two related principal eigenvalues and the domain size, the advection rate as well as the diffusion rate. Our main results are presented in Section 3. To illustrate our results, we also present some numerical simulations in Section 4. We conclude this paper in the last section.

2. Useful lemmas

In order to discuss the existence of $(\widetilde{u}, 0)$, corresponding to systems (1.5) and (1.7), we need to study the following subsystems:

$$\begin{cases} \dfrac{\partial u}{\partial t} = du_{xx} - \alpha u_x + u[b_1(x) - \delta_1 u], & t > 0, x \in (0, L), \\ du_x(0, t) - \alpha u(0, t) = 0, & t > 0, \\ du_x(L, t) - \alpha u(L, t) = -\beta\alpha u(L, t), & t > 0, \\ u(x, 0) = u_0(x) \geq, \not\equiv 0, & x \in [0, L], \end{cases} \tag{2.1}$$

and

$$\begin{cases} \dfrac{\partial u}{\partial t} = du_{xx} - \alpha u_x + u[b_1(x) - \delta_1 u], & t > 0, x \in (0, L), \\ du_x(0, t) - \alpha u(0, t) = 0, & t > 0, \\ u(L, t) = 0, & t > 0, \\ u(x, 0) = u_0(x) \geq, \not\equiv 0, & x \in [0, L], \end{cases} \tag{2.2}$$

respectively.

This leads to the study of the following linear eigenvalue problem

$$\begin{cases} d\phi_{xx} - \alpha\phi_x + \phi b_1(x) = \sigma\phi, & x \in (0, L), \\ d\phi_x(0) - \alpha\phi(0) = 0, \\ d\phi_x(L) - \alpha\phi(L) = -\beta\alpha\phi(L). \end{cases} \tag{2.3}$$

In the case that $\beta = +\infty$, the corresponding eigenvalue problem reads as

$$\begin{cases} d\phi_{xx} - \alpha\phi_x + \phi b_1(x) = \sigma\phi, & x \in (0, L), \\ d\phi_x(0) - \alpha\phi(0) = 0, \\ \phi(L) = 0. \end{cases} \tag{2.4}$$

Throughout this paper, we denote the principal eigenvalue of (2.3) or (2.4) by $\sigma_1(\alpha, d, L)$.

2.1. Dependence of $\sigma_1(\alpha, d, L)$ on α, d and L

First, we shall investigate how $\sigma_1(\alpha, d, L)$ depends on α.

Lemma 2.1. *Suppose that (1.6) is satisfied, then*

(a) When $\beta \in (0, \frac{1}{2})$, if $b_1'(x) \leq 0$, then $\sigma_1(\alpha, d, L)$ is a strictly monotone decreasing function of α; When $\beta \in [\frac{1}{2}, +\infty]$, then $\sigma_1(\alpha, d, L)$ is a strictly monotone decreasing function of α.

(b) $0 < \underline{b} \leq \lim_{\alpha\to 0} \sigma_1(\alpha, d, L) \leq \bar{b}$ provided that $\beta < +\infty$.

(c) $\lim_{\alpha\to+\infty} \sigma_1(\alpha, d, L) = -\infty$.

Proof. Set $\varphi = e^{-\frac{\alpha}{d}x}\phi$, then (2.3) becomes

$$\begin{cases} d\varphi_{xx} + \alpha\varphi_x + b_1(x)\varphi = \sigma\varphi, \quad x \in (0, L), \\ \varphi_x(0) = 0, \\ d\varphi_x(L) = -\beta\alpha\varphi(L), \end{cases} \tag{2.5}$$

and (2.4) becomes

$$\begin{cases} d\varphi_{xx} + \alpha\varphi_x + b_1(x)\varphi = \sigma\varphi, \quad x \in (0, L), \\ \varphi_x(0) = 0 = \varphi(L). \end{cases} \tag{2.6}$$

Let us denote by φ_α the derivative of φ with respect to α. Multiplying the first equation of (2.5) by $e^{\frac{\alpha}{d}x}\varphi_\alpha$, we obtain

$$d(e^{\frac{\alpha}{d}x}\varphi_x)_x\varphi_\alpha + \varphi\varphi_\alpha e^{\frac{\alpha}{d}x}b_1(x) = \sigma\varphi\varphi_\alpha e^{\frac{\alpha}{d}x}. \tag{2.7}$$

Integrating (2.7) over $(0, L)$ yields

$$\int_0^L d(e^{\frac{\alpha}{d}x}\varphi_x)_x\varphi_\alpha = \int_0^L (\sigma - b_1(x))\varphi\varphi_\alpha e^{\frac{\alpha}{d}x}. \tag{2.8}$$

On the other hand, it follows from (2.5) that

$$\begin{cases} d\varphi_{\alpha xx} + \varphi_x + \alpha\varphi_{\alpha x} + b_1(x)\varphi_\alpha = \sigma_\alpha\varphi + \sigma\varphi_\alpha, \\ d\varphi_{\alpha x}(0) = 0, \\ d\varphi_{\alpha x}(L) = -\beta\varphi(L) - \beta\alpha\varphi_\alpha(L). \end{cases} \tag{2.9}$$

Multiplying (2.9) by $e^{\frac{\alpha}{d}x}\varphi(x)$ and integrating it over $(0, L)$, we have

$$\int_0^L d(e^{\frac{\alpha}{d}x}\varphi_{\alpha x})_x\varphi + \int_0^L e^{\frac{\alpha}{d}x}\varphi_x\varphi = \int_0^L (\sigma - b_1(x))\varphi\varphi_\alpha e^{\frac{\alpha}{d}x} + \sigma_\alpha \int_0^L \varphi^2 e^{\frac{\alpha}{d}x}. \tag{2.10}$$

Using integration by parts and (2.8), we obtain

$$\sigma_\alpha = \frac{-e^{\frac{\alpha}{d}L}\beta\varphi^2(L) + \int_0^L e^{\frac{\alpha}{d}x}\varphi_x\varphi}{\int_0^L \varphi^2 e^{\frac{\alpha}{d}x}}. \tag{2.11}$$

If $\beta = +\infty$, (2.11) becomes

$$\sigma_\alpha = \frac{\int_0^L e^{\frac{\alpha}{d}x}\varphi_x\varphi}{\int_0^L \varphi^2 e^{\frac{\alpha}{d}x}}. \tag{2.12}$$

In general, when $\beta \in (0, \frac{1}{2})$, $\sigma_1(\alpha, d, L)$ may not be monotone in α. To ensure $\sigma_\alpha < 0$, we need to show $\varphi_x < 0$ in $(0, L)$. To this end, we set $W = \frac{\phi_x}{\phi}$, and we can rewrite (2.3) as the following equation

$$\begin{cases} dW_{xx} + (2dW - \varphi)W_x = -b_1'(x), \\ W(0) = \frac{\alpha}{d}, \ W(L) = (1 - \beta)\frac{\alpha}{d}. \end{cases} \tag{2.13}$$

Since $b_1'(x) \leq 0$, then by the maximum principle we have $W < \frac{\alpha}{d}$, which implies that $\varphi_x < 0$ in $(0, L)$ ([18]). This implies that $\sigma_1(\alpha, d, L)$ is a strictly monotone decreasing function of α.

For the case $\beta \in [\frac{1}{2}, +\infty)$, from (2.11), we have $\sigma_\alpha = \frac{-e^{\frac{\alpha}{d}L}\beta\varphi^2(L)+\int_0^L e^{\frac{\alpha}{d}x}\varphi_x\varphi}{\int_0^L \varphi^2 e^{\frac{\alpha}{d}x}}$
$= \frac{-e^{\frac{\alpha}{d}L}\beta\varphi^2(L)+\int_0^L e^{\frac{\alpha}{d}x} d\frac{\varphi^2}{2}}{\int_0^L \varphi^2 e^{\frac{\alpha}{d}x}} = \frac{-e^{\frac{\alpha}{d}L}\beta\varphi^2(L)+e^{\frac{\alpha}{d}x}\frac{\varphi^2}{2}|_0^L - \frac{\alpha}{d}\int_0^L e^{\frac{\alpha}{d}x}\frac{\varphi^2}{2}}{\int_0^L \varphi^2 e^{\frac{\alpha}{d}x}} = \frac{-(\beta-\frac{1}{2})e^{\frac{\alpha}{d}L}\varphi^2(L) - \frac{\varphi^2(0)}{2} - \frac{\alpha}{d}\int_0^L e^{\frac{\alpha}{d}x}\frac{\varphi^2}{2}}{\int_0^L \varphi^2 e^{\frac{\alpha}{d}x}}$.

It is easy to see $\beta \in [\frac{1}{2}, +\infty)$ implies that $\sigma_\alpha < 0$. When $\beta = +\infty$, Using the same calculation as above and combining with (2.12), we can obtain that $\sigma_\alpha < 0$.

If $\alpha = 0$, then the boundary condition of (2.5) is simply a Neumann boundary condition. Furthermore, combining with (1.6), we have

$$0 < \underline{b} \leq \lim_{\alpha \to 0} \sigma_1(\alpha, d, L) \leq \bar{b}.$$

Especially, $\lim_{\alpha \to 0} \sigma_1(\alpha, d, L) = b_1$, when $b_1(x) = b_1$. It follows from Proposition 2.1 of [19] and (1.6) that

$$\sigma_1(\alpha, d, L) \leq \left(\gamma^2 - \gamma\right)\frac{\alpha^2}{d} + \bar{b},$$

where $0 < \gamma < \min\{1, \beta\}$. Consequently, $\lim_{\alpha \to +\infty} \sigma_1(\alpha, d, L) = -\infty$. □

Next we investigate the relationship between $\sigma_1(\alpha, d, L)$ and L.

Lemma 2.2. *$\sigma_1(\alpha, d, L)$ is a strictly monotone increasing function of L.*

Proof. First we consider system (2.5) by fixing the parameters α and d and varying L. For any $0 < L_1 < L_2$, we show that $\sigma_1(\alpha, d, L_1) < \sigma_1(\alpha, d, L_2)$. Let φ_1 be the positive eigenfunction corresponding to $\sigma_1(\alpha, d, L_1)$, and define

$$\psi = \begin{cases} \varphi_1, & 0 < x \leq L_1 \\ 0, & L_1 < x < L_2. \end{cases}$$

Since

$$\begin{aligned}
& \sigma_1(\alpha, d, L_1) \\
= & \frac{-\beta\alpha e^{\frac{\alpha}{d}L_1}\varphi_1^2(L_1) - \beta_1\alpha\varphi_1^2(0) - d\int_0^{L_1} e^{\frac{\alpha}{d}x}(\varphi_{1x})^2 dx + \int_0^{L_1} b_1(x)e^{\frac{\alpha}{d}x}\varphi_1^2 dx}{\int_0^{L_1} e^{\frac{\alpha}{d}x}\varphi_1^2 dx} \\
= & \frac{-\beta\alpha e^{\frac{\alpha}{d}L_2}\psi^2(L_2) - \beta_1\alpha\psi^2(0) - d\int_0^{L_2} e^{\frac{\alpha}{d}x}(\psi_x)^2 dx + \int_0^{L_2} b_1(x)e^{\frac{\alpha}{d}x}\psi^2 dx}{\int_0^{L_2} e^{\frac{\alpha}{d}x}\psi^2 dx} \\
\leq & \max_{\psi \neq 0, \psi \in W^{1,2}} \frac{-\beta\alpha e^{\frac{\alpha}{d}L_2}\psi^2(L_2) - \beta_1\alpha\psi^2(0) - d\int_0^{L_2} e^{\frac{\alpha}{d}x}(\psi_x)^2 dx + \int_0^{L_2} b_1(x)e^{\frac{\alpha}{d}x}\psi^2 dx}{\int_0^{L_2} e^{\frac{\alpha}{d}x}\psi^2 dx} \\
= & \sigma_1(\alpha, d, L_2).
\end{aligned}$$

Due to the strict positivity of the eigenfunction corresponding to $\sigma_1(\alpha, d, L_2)$ in $[0, L_2]$, the above inequality should be strict, which implies $\sigma_1(\alpha, d, L_1) < \sigma_1(\alpha, d, L_2)$. The case with $\beta = +\infty$ can be dealt with in a similar fashion and we skip the details here. □

Lemma 2.3. *Assume (1.6) holds. If $\beta = +\infty$, then $\sigma_1(\alpha, d, L) \to -\infty$ as $L \to 0$.*

Proof. We rewrite $\sigma_1(\alpha, d, L)$ as $\sigma_1(\alpha, d, L, b_1(x))$ to emphasize the dependence of $\sigma_1(\alpha, d, L)$ on the function $b_1(x)$. By Corollary 2.2 of [20], one easily sees that $\sigma_1(\alpha, d, L, b_1(x)) \le \sigma_1(\alpha, d, L, \bar{b})$.

Next we consider the following boundary value problem (BVP)

$$\begin{cases} d\phi_{xx} - \alpha\phi_x + \phi\bar{b} = \sigma\phi, \quad x \in (0, L), \\ d\phi_x(0) - \alpha\phi(0) = 0, \\ \phi(L) = 0. \end{cases} \tag{2.14}$$

Set $\psi = e^{-\frac{\alpha x}{2d}}\phi$, then (2.14) yields

$$\begin{cases} d\psi_{xx} + [\bar{b} - \dfrac{\alpha^2}{4d} - \sigma]\psi = 0, \quad x \in (0, L), \\ \psi_x(0) - \frac{\alpha}{2d}\psi(0) = 0, \\ \psi(L) = 0, \end{cases} \tag{2.15}$$

From the boundary conditions we find

$$\tan \frac{\sqrt{4d(\bar{b} - \sigma_1) - \alpha^2}}{2d} L + \frac{\sqrt{4d(\bar{b} - \sigma_1) - \alpha^2}}{\alpha} = 0, \text{ for } 4d(\bar{b} - \sigma_1) > \alpha^2. \tag{2.16}$$

Since by Lemma 2.2, we have

$$\lim_{L \to 0^+} \sigma_1(\bar{b}) = \sigma^* \in R \cup \{-\infty\}.$$

Assume that σ^* is finite, then from (2.16), we obtain $\sigma^* = \frac{4d\bar{b} - \alpha^2}{4d}$, and hence $\psi(x) = Ax + B$. The boundary conditions imply that $A = B = 0$. This is impossible. Thus $\lim_{L \to 0^+} \sigma_1(\bar{b}) = -\infty$ and hence $\lim_{L \to 0^+} \sigma_1(b_1(x)) = -\infty$. □

Lemma 2.4. *If $\beta = +\infty$ and $\alpha = 0$, then $\sigma_1(\alpha, d, L)$ is a strictly monotone decreasing function of d.*

Proof. Let us denote by φ_d the derivative of φ with respect to d. Multiplying the first equation of (2.6) by $e^{\frac{\alpha}{d}x}\varphi_d$, it holds that

$$d(e^{\frac{\alpha}{d}x}\varphi_x)_x\varphi_d + \varphi\varphi_d e^{\frac{\alpha}{d}x} b_1(x) = \sigma\varphi\varphi_d e^{\frac{\alpha}{d}x}. \tag{2.17}$$

Integrating (2.17) over $(0, L)$, we obtain

$$\int_0^L d(e^{\frac{\alpha}{d}x}\varphi_x)_x\varphi_d = \int_0^L (\sigma - b_1(x))\varphi\varphi_d e^{\frac{\alpha}{d}x}. \tag{2.18}$$

On the other hand, it follows from (2.6) that

$$\begin{cases} \varphi_{xx} + d\varphi_{dxx} + \alpha\varphi_{dx} + b_1(x)\varphi_d = \sigma_d\varphi + \sigma\varphi_d, \\ \varphi_{dx}(0) = 0 \ or\ \varphi_d(0) = 0, \\ \varphi_d(L) = 0. \end{cases} \tag{2.19}$$

Multiplying (2.19) by $e^{\frac{\alpha}{d}x}\varphi(x)$ and integrating it over $(0, L)$, we have

$$\int_0^L d(e^{\frac{\alpha}{d}x}\varphi_{dx})_x\varphi + \int_0^L e^{\frac{\alpha}{d}x}\varphi_{xx}\varphi = \int_0^L (\sigma - b_1(x))\varphi\varphi_d e^{\frac{\alpha}{d}x} + \sigma_d \int_0^L \varphi^2 e^{\frac{\alpha}{d}x}. \tag{2.20}$$

Using integration by parts and (2.18), we obtain

$$\sigma_d = \frac{-\int_0^L e^{\frac{\alpha}{d}x}(\varphi_x)^2 - \frac{\alpha}{d}\int_0^L e^{\frac{\alpha}{d}x}\varphi\varphi_x}{\int_0^L \varphi^2 e^{\frac{\alpha}{d}x}}. \tag{2.21}$$

We find $\sigma_d < 0$, when $\alpha = 0$. □

If $\beta = +\infty$, we also have the following remark (See Theorem 3.1 of [21]).

Remark 2.5. *(i)* $\sigma_1(0, d, L) \to \max_{x\in[0,L]} b_1(x) > 0$ *as* $d \to 0$*;*

(ii) $\sigma_1(0, d, L) \to -\infty$ *as* $d \to +\infty$.

3. Main results

Our first result is the following theorem.

Theorem 3.1. *If system (1.5) admits a semi-trivial steady state* $(\widetilde{u}, 0)$*, then the semi-trivial steady state* $(\widetilde{u}, 0)$ *is locally asymptotically stable.*

Proof. Linearizing the second equation of system (1.5) at $(\widetilde{u}, 0)$, we obtain the following eigenvalue problem

$$\begin{cases} d\phi_{xx} - \alpha\phi_x - \delta_2\widetilde{u}\phi = \zeta\phi, & in\ \ (0, L), \\ d\phi_x(0) - \alpha\phi(0) = \beta\alpha\phi(0), \\ d\phi_x(L) - \alpha\phi(L) = -\beta\alpha\phi(L). \end{cases} \tag{3.1}$$

Let $\widetilde{\phi} = e^{-\frac{\alpha}{d}x}\phi$, then problem (3.1) becomes

$$\begin{cases} d(e^{\frac{\alpha}{d}x}\widetilde{\phi}_x)_x - \delta_2 e^{\frac{\alpha}{d}x}\widetilde{u}\widetilde{\phi} = \zeta e^{\frac{\alpha}{d}x}\widetilde{\phi}, & in\ \ (0, L), \\ d\widetilde{\phi}_x(0) = \beta\alpha\widetilde{\phi}(0), \\ d\widetilde{\phi}_x(L) = -\beta\alpha\widetilde{\phi}(L). \end{cases} \tag{3.2}$$

By the variational method, ζ_1 can be characterized by

$$\zeta_1 = \frac{-\beta\alpha\widetilde{\phi_1}^2(0) - \beta\alpha e^{\frac{\alpha L}{d}}\widetilde{\phi_1}^2(L) - d\int_0^L e^{\frac{\alpha}{d}x}(\widetilde{\phi}_{1x})^2 - \int_0^L \delta_2 e^{\frac{\alpha}{d}x}\widetilde{u}(\widetilde{\phi_1})^2}{\int_0^L e^{\frac{\alpha}{d}x}(\widetilde{\phi_1})^2} \tag{3.3}$$

and when $\beta = +\infty$,

$$\zeta_1 = \frac{-d\int_0^L e^{\frac{\alpha}{d}x}(\widetilde{\phi}_{1x})^2 - \int_0^L \delta_2 e^{\frac{\alpha}{d}x}\widetilde{u}(\widetilde{\phi_1})^2}{\int_0^L e^{\frac{\alpha}{d}x}(\widetilde{\phi_1})^2}, \tag{3.4}$$

where $\widetilde{\phi_1}$ is the eigenfunction associated with ζ_1. Thus $\zeta_1 < 0$ and it follows from Proposition 3.1 of [20] that the semi-trivial steady state $(\widetilde{u}, 0)$ is locally asymptotically stable. □

Theorem 3.2. *If* $\alpha = 0$*, or* $\alpha > 0$ *and* $\beta = 0$*, then system (1.5) admits a semi-trivial steady state,* $(\widetilde{u}, 0)$*, which is locally asymptotically stable, where* $\widetilde{u}$ *is the unique positive steady state of problem (2.1).*

Proof. Under the assumptions, the linear eigenvalue problem (2.3) reads as

$$\begin{cases} d\phi_{xx} + \phi b_1(x) = \lambda\phi, & x \in (0, L), \\ \phi_x(0) = 0 = \phi_x(L), \end{cases} \tag{3.5}$$

and

$$\begin{cases} d\phi_{xx} - \alpha\phi_x + \phi b_1(x) = \eta\phi, & x \in (0, L), \\ d\phi_x(0) - \alpha\phi(0) = 0, \\ d\phi_x(L) - \alpha\phi(L) = 0, \end{cases} \tag{3.6}$$

respectively. For (3.5), a standard eigenvalue analysis gives the principle eigenvalue

$$\lambda_1 = \max_{\phi \in W^{1,2}(0,L), \phi \neq 0} \left[\frac{-d \int_0^L (\phi_x)^2 + \int_0^L b_1(x)(\phi)^2}{\int_0^L (\phi)^2} \right]. \tag{3.7}$$

Moreover, it is easy to verify that $\lambda_1 > 0$ by using the test function $\phi = 1$. For (3.6), we multiply the equations by $e^{-\frac{\alpha}{d}x}$ to get

$$\begin{cases} d(e^{-\frac{\alpha}{d}x}\phi_x)_x + e^{-\frac{\alpha}{d}x}\phi b_1(x) = \eta e^{-\frac{\alpha}{d}x}\phi, & x \in (0, L), \\ (e^{-\frac{\alpha}{d}x}\phi)_x(x) = 0, & x = 0, L. \end{cases} \tag{3.8}$$

Thus the associated principle eigenvalue is

$$\eta_1 = \max_{\phi \in W^{1,2}(0,L), \phi \neq 0} \left[\frac{\alpha e^{-\frac{\alpha}{d}L}\phi^2(L) - \alpha\phi^2(0) - d \int_0^L e^{-\frac{\alpha}{d}x}(\phi_x)^2 + \int_0^L e^{-\frac{\alpha}{d}x} b_1(x)(\phi)^2}{\int_0^L e^{-\frac{\alpha}{d}x}(\phi)^2} \right].$$

Using the test function $\phi \equiv e^{\frac{\alpha}{d}x}$, we see that $\eta_1 > 0$. The conclusion then follows from Propositions 3.2 and 3.3 of [20] and Theorem 3.1. □

For the spatially homogeneous case, by Lemmas 2.1 and 2.2, Theorems 2.1 and 2.3 of [19], we have the following result.

Theorem 3.3. *Assume that $b_1(x) \equiv b_1 > 0$ is a constant.*

(a) If $\beta \in (0, \frac{1}{2})$ and $0 < \alpha < \sqrt{\frac{db_1}{\beta(1-\beta)}}$, then system (1.5) admits a semi-trivial steady state, $(\widetilde{u}, 0)$, with $\widetilde{u}$ being the unique positive steady state of problem (2.1), if and only if $L > L_1^*$, where

$$L_1^* = \begin{cases} \dfrac{2d \arctan \frac{\alpha\beta\sqrt{4db_1-\alpha^2}}{2db_1-\alpha^2\beta}}{\sqrt{4db_1-\alpha^2}}, & \text{if } 0 < \alpha \le \sqrt{4db_1}, \\ \dfrac{d}{\sqrt{\alpha^2-4db_1}} \ln \dfrac{2db_1-\beta\alpha^2+\alpha\beta\sqrt{\alpha^2-4db_1}}{2db_1-\beta\alpha^2-\alpha\beta\sqrt{\alpha^2-4db_1}}, & \text{if } \sqrt{4db_1} < \alpha < \sqrt{\frac{db_1}{\beta(1-\beta)}}. \end{cases}$$

Moreover, if $\alpha \ge \sqrt{\frac{db_1}{\beta(1-\beta)}}$, then problem (2.1) only has a globally asymptotically stable zero steady state and system (1.5) does not admit a semi-trivial steady state in the form of $(\widetilde{u}, 0)$ satisfying $\widetilde{u} > 0$.

(b) *When* $\beta = \frac{1}{2}$. *If* $0 < \alpha < \sqrt{4db_1}$, *then system (1.5) admits a semi-trivial steady state,* $(\widetilde{u}, 0)$, *with* $\widetilde{u}$ *being the unique positive steady state of problem (2.1), if and only if* $L > L_1^*$ *with*

$$L_1^* = \frac{2d \arctan \frac{\alpha\sqrt{4db_1-\alpha^2}}{4db_1-\alpha^2}}{\sqrt{4db_1-\alpha^2}}.$$

If $\alpha \geq \sqrt{4db_1}$, *then system (1.5) does not admit a semi-trivial steady state in the form of* $(\widetilde{u}, 0)$ *satisfying* $\widetilde{u} > 0$.

(c) *Suppose* $\beta \in (\frac{1}{2}, +\infty)$. *If* $0 < \alpha < \sqrt{4db_1}$, *then system (1.5) admits a semi-trivial steady state,* $(\widetilde{u}, 0)$, *with* $\widetilde{u}$ *being the unique positive steady state of problem (2.1), if and only if* $L > L_1^*$ *with*

$$L_1^* = \begin{cases} \dfrac{2d \arctan \frac{\alpha\beta\sqrt{4db_1-\alpha^2}}{2db_1-\alpha^2\beta}}{\sqrt{4db_1-\alpha^2}}, & \text{if } 0 < \alpha \leq \sqrt{\frac{2db_1}{\beta}}, \\ 2d\dfrac{\pi + \arctan \frac{\alpha\beta\sqrt{4db_1-\alpha^2}}{2db_1-\alpha^2\beta}}{\sqrt{4db_1-\alpha^2}}, & \text{if } \sqrt{\frac{2db_1}{\beta}} < \alpha < \sqrt{4db_1}. \end{cases}$$

If $\alpha \geq \sqrt{4db_1}$, *then system (1.5) does not admit a semi-trivial steady state in the form of* $(\widetilde{u}, 0)$ *satisfying* $\widetilde{u} > 0$.

(d) *Suppose that* $\beta \in (0, \frac{1}{2})$. *If* $d > \frac{\alpha^2\beta(1-\beta)}{b_1}$, *then system (1.5) admits a semi-trivial steady state,* $(\widetilde{u}, 0)$, *with* $\widetilde{u}$ *being the unique positive steady state of problem (2.1), if and only if* $L > L_1^*$ *with*

$$L_1^* = \begin{cases} \dfrac{2d \arctan \frac{\alpha\beta\sqrt{4db_1-\alpha^2}}{2db_1-\alpha^2\beta}}{\sqrt{4db_1-\alpha^2}}, & \text{if } d \geq \frac{\alpha^2}{4b_1}, \\ \dfrac{d}{\sqrt{\alpha^2-4db_1}} \ln \dfrac{2db_1-\beta\alpha^2+\alpha\beta\sqrt{\alpha^2-4db_1}}{2db_1-\beta\alpha^2-\alpha\beta\sqrt{\alpha^2-4db_1}}, & \text{if } \frac{\alpha^2\beta(1-\beta)}{b_1} < d < \frac{\alpha^2}{4b_1}. \end{cases}$$

(e) *For* $\beta = \frac{1}{2}$, *if* $d > \frac{\alpha^2}{4b_1}$, *then system (1.5) admits a semi-trivial steady state,* $(\widetilde{u}, 0)$, *with* $\widetilde{u}$ *being the unique positive steady state of problem (2.1), if and only if* $L > L_1^* = \dfrac{2d \arctan \frac{\alpha\beta\sqrt{4db_1-\alpha^2}}{2db_1-\alpha^2\beta}}{\sqrt{4db_1-\alpha^2}}$.

(f) *Suppose that* $\beta \in (\frac{1}{2}, +\infty)$, *when* $d > \frac{\alpha^2}{4b_1}$, *then system (1.5) admits a semi-trivial steady state,* $(\widetilde{u}, 0)$, *with* $\widetilde{u}$ *being the unique positive steady state of problem (2.1), if and only if* $L > L_1^*$, *where* L_1^* *is given by*

$$L_1^* = \begin{cases} \dfrac{2d \arctan \frac{\alpha\beta\sqrt{4db_1-\alpha^2}}{2db_1-\alpha^2\beta}}{\sqrt{4db_1-\alpha^2}}, & d \geq \frac{\alpha^2\beta}{2b_1}, \\ 2d\dfrac{\pi + \arctan \frac{\alpha\beta\sqrt{4db_1-\alpha^2}}{2db_1-\alpha^2\beta}}{\sqrt{4db_1-\alpha^2}}, & \frac{\alpha^2}{4b_1} < d < \frac{\alpha^2\beta}{2b_1}. \end{cases}$$

(g) *For any $\alpha > 0$, $\beta \in (0,1)$, if $d \le \tilde{d}$, then system (1.5) does not admit a semi-trivial steady state in the form of $(\widetilde{u}, 0)$ satisfying $\widetilde{u} > 0$, where*

$$\tilde{d} = \begin{cases} \frac{\alpha^2\beta(1-\beta)}{b_1}, & 0 < \beta < \frac{1}{2} \\ \frac{\alpha^2}{4b_1}, & \frac{1}{2} \le \beta < 1. \end{cases}$$

Similarly, for system (1.7), we have the following result.

Theorem 3.4. *Suppose $b_1(x) \equiv b_1 > 0$ is a constant. Then we have the following conclusions.*

(i) *For any $d > 0$, if $0 < \alpha < \sqrt{4b_1 d}$, then there exists a critical number*

$$\widehat{L_1^*} = \frac{2d(\pi + \arctan\frac{-\sqrt{4db_1-\alpha^2}}{\alpha})}{\sqrt{4db_1 - \alpha^2}}$$

such that for $L \ge \widehat{L_1^*}$, system (1.7) admits a stable semi-trivial steady state $(\widetilde{u}, 0)$, where $\widetilde{u} > 0$ is the unique positive steady state of system (2.2). Moreover, $\widehat{L_1^*}$ is an increasing function of the advection rate α for $0 < \alpha < \sqrt{4b_1 d}$.

(ii) *For any α, if $d > \frac{\alpha^2}{4b_1}$, then there exists a critical number*

$$\widehat{L_1^*} = \frac{2d(\pi + \arctan\frac{-\sqrt{4db_1-\alpha^2}}{\alpha})}{\sqrt{4db_1 - \alpha^2}}$$

such that for $L \ge \widehat{L_1^*}$, system (1.7) admits a stable semi-trivial steady state $(\widetilde{u}, 0)$, where $\widetilde{u} > 0$ is the unique positive steady state of system (2.2). Further, $\widehat{L_1^*}$ is an decreasing function of the diffusion rate d, for $\frac{\alpha^2}{4b_1} < d < \frac{\alpha^2}{2b_1}$.

(iv) *If $\alpha \ge \sqrt{4b_1 d}$, then system (1.7) does not admit a semi-trivial steady state in the form of $(\widetilde{u}, 0)$, where $\widetilde{u} > 0$.*

If $b_1(x)$ is not a constant, we have the following result.

Theorem 3.5. *Suppose that (1.6) is satisfied. Then the following conclusions hold.*

(I) *If $\alpha > 0$, when $\beta \in (0, \frac{1}{2})$, $b_1'(x) \le 0$, or $\beta \in [\frac{1}{2}, +\infty)$, then there exists $\alpha^* > 0$ such that for $0 < \alpha < \alpha^*$, system (1.5) admits a semi-trivial steady state, $(\widetilde{u}, 0)$, which is stable, and $\widetilde{u}$ is the unique positive steady state of problem (2.1).*

(II) *For the case with $\beta = \infty$, we have the following conclusions.*

(II.1) *If $\alpha = 0$, then there exists d^* such that for $0 < d < d^*$, system (1.7) admits a semi-trivial steady state $(\widetilde{u}, 0)$, which is stable and $\widetilde{u}$ is the unique positive steady state of system (2.2).*

(II.2) *If $L > \frac{\pi}{2}\sqrt{\frac{d}{b}}$, then there exists $\tilde{\alpha}^*$ such that for $0 < \alpha < \tilde{\alpha}^*$, system (1.7) admits a semi-trivial steady state $(\widetilde{u}, 0)$, which is stable and $\widetilde{u}$ is the unique positive steady state of system (2.2).*

(II.3) If $0 < \alpha < \sqrt{4\underline{b}d}$, then there exists a $L^* > 0$ such that for $L > L^*$, system (1.7) admits a semi-trivial steady state $(\widetilde{u}, 0)$, which is stable and $\widetilde{u}$ is the unique positive steady state of system (2.2).

Proof. The case (I) can be proved by (a), (b) and (c) of Lemma 2.1 and the proof of case (II.1) can be obtained by Lemma 2.4 and Remark 2.5. To prove case (II.2), we just need to verify the following three facts.

(1) $\sigma_1(\alpha, b_1(x))$ is a strictly monotone decreasing function of α;

(2) $\lim_{\alpha\to 0} \sigma_1(\alpha, b_1(x)) > 0$;

(3) $\lim_{\alpha\to +\infty} \sigma_1(\alpha, b_1(x)) = -\infty$.

Note that (1) and (3) follow immediately from Lemma 2.1. Furthermore, (2) follows from noting that $\sigma_1(0, b_1(x)) \geq \sigma_1(0, \underline{b})$ for $b_1(x) \geq \underline{b}$ and $\sigma_1(0, b_1(x)) \geq \sigma_1(0, \underline{b}) = \underline{b} - \frac{d\pi^2}{4L^2} > 0$, when $\beta = +\infty$ and $L > \frac{\pi}{2}\sqrt{\frac{d}{\underline{b}}}$.

Next we prove (II.3). Note that $\beta = \infty$, the associated eigenvalue problem is

$$\begin{cases} d\phi_{xx} - \alpha\phi_x + \phi\underline{b} = \sigma_1\phi, \quad x \in (0, L), \\ d\phi_x(0) - \alpha\phi(0) = 0, \\ \phi(L) = 0, \end{cases} \tag{3.9}$$

where ϕ is corresponding eigenfunction of σ_1.

If $0 < \alpha < \sqrt{4\underline{b}d}$, then it follows from Theorem 3.4 that $\sigma_1(\underline{b}) > 0$, as $L \to +\infty$. Hence, it is easy to know that $\sigma_1(b_1(x)) > 0$, as $L \to +\infty$, if $0 < \alpha < \sqrt{4\underline{b}d}$. Therefore the proof of case (II.3) follows directly from Lemma 2.2 and Lemma 2.3. □

4. Numerical simulations

In this section, we use several numerical simulations to illustrate our theoretical results. First we verify Theorem 3.3. We take parameter values: $\beta = 0.4$, $b_1(x) = 0.1077$, $b_2(x) = 0.1988$, $\delta_1 = \delta_2 = 8.5034 \times 10^{-6}$, $d = 1.25 \times 10^{-2}$, $\alpha = 1.25 \times 10^{-2}$. For this set of parameters, we find that $\alpha < \sqrt{\frac{db_1}{\beta(1-\beta)}} \approx 0.0749$ and $L_1^* \approx 0.0472$. Theorem 3.3 applies here: if we take $L = 0.04 < L_1^*$, then as shown in Figure 1 (Left), the solution of (1.5) approaches the trivial steady state $(0, 0)$, while if we take $L = 0.05 > L_1^*$, as shown in Figure 1 (Right), the solution of (1.5) approaches the semi-trivial steady state $(\widetilde{u}, 0)$ implying that all mosquitoes are infected with *Wolbachia*.

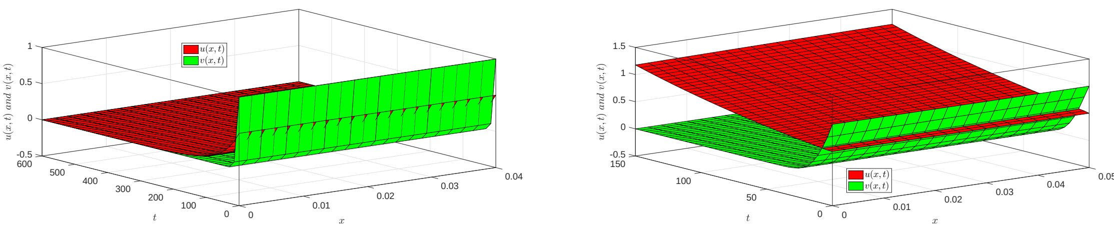

Figure 1. Numerical solutions of system (1.5). Initial conditions were chosen as: $u_0 = 0.5, v_0 = 1$. (Left) $L = 0.04$; (Right) $L = 0.05$.

Now we take parameter values as: $d = 1.25 \times 10^{-2}$, $\delta_1 = \delta_2 = 8.5034 \times 10^{-6}$, $b_1(x) = e^{-x} + 1$, $b_2(x) = 1.5 + \sin(x)$, $\beta = 0.4$, $L = 0.1$. For this set of parameters, we can numerically find $\alpha* \approx 0.261$ such that the solutions of (1.5) approach $(\widetilde{u}, 0)$ if $\alpha \in [0, \alpha^*)$, and approach $(0, 0)$ if $\alpha \geq \alpha^*$ (See Figure 2).

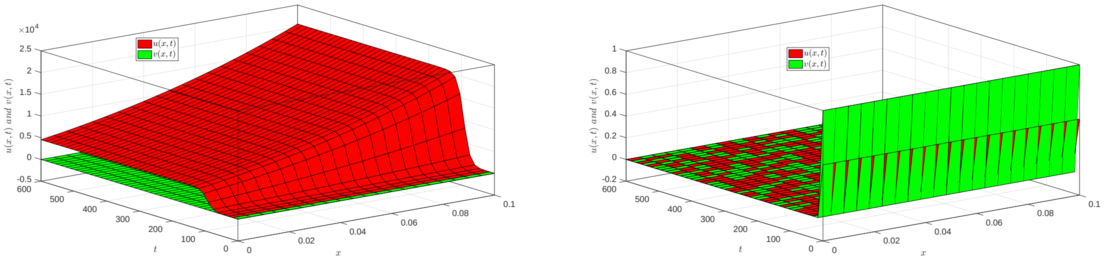

Figure 2. Numerical solutions of system (1.7). Initial conditions were chosen as: $u_0 = 0.5, v_0 = 1$. (Left) $\alpha = 0.25 < \alpha^*$; (Right) $\alpha = 0.27 > \alpha^*$.

Now we take $\beta = \infty$, $\alpha = 0.1789$, $d = 1.25 \times 10^{-2}$, $\delta_1 = \delta_2 = 0.85034 \times 10^{-6}$, $b_1(x) = e^{-x} + 1$, $b_2(x) = e^{-x} + 1$. Then $\underline{b} = 1$, $\alpha < \sqrt{4d\underline{b}} = 0.2236$. Numerically we find $\hat{L}^* \approx 0.21$. As shown in Figure 3, if $L > L_1^*$, then the solutions of (1.5) approach the semi-trivial steady state $(\widetilde{u}, 0)$ implying a full establishment *Wolbachia* is achieved, while the establishment of *Wolbachia* fails if $L < L_1^*$.

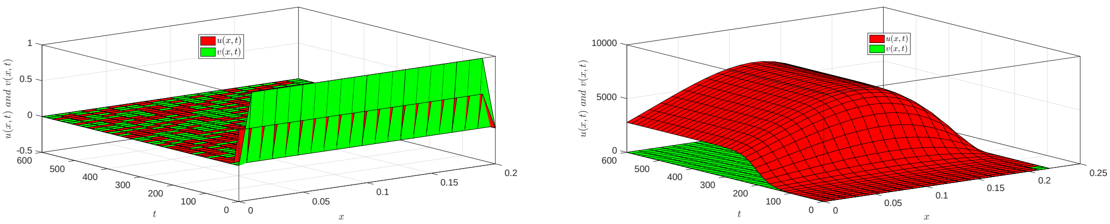

Figure 3. Numerical solutions of system (1.7). Initial conditions were chosen as: $u_0 = 0.5, v_0 = 1$. (Left) $L = 0.20 < L_1^*$; (Right) $L = 0.22 > L_1^*$.

5. Conclusions

In this paper, we have proposed a reaction-diffusion-advection model in one-dimensional spatially inhomogeneous environment with general boundary conditions. Our results (Theorems 3.2–3.5) show that in order to fully establish *Wolbachia* in the wild mosquito population, i.e., all mosquitoes eventually carry *Wolbachia*, the wind related parameter α and the patch size L over which the mosquitoes with *Wolbachia* are spreading should satisfy certain requirements. Generally speaking, the wind cannot be too strong, and the minimum patch size cannot be too small. The critical values of the advection parameter α and the patch size L for the establishment of *Wolbachia* depend on the model parameters including the diffusion rate d, the birth rates $b_1(x)$ and $b_2(x)$, and the death rates δ_1 and δ_2. For instance, Theorem 3.3 (a) indicates, if $b_1(x) = b_1$ is a positive constant and $\beta \in (0, 1/2)$, then the full establishment of *Wolbachia* will not be successful if α is too large such that $\alpha \geq \sqrt{\frac{db_1}{\beta(1-\beta)}}$ (i.e.,the wind is too strong) or if α is in a proper range ($0 < \alpha < \sqrt{\frac{db_1}{\beta(1-\beta)}}$), but the patch size L is too small satisfying

$L < L_1^*$ (See Figure 1).

Acknowledgements

The authors wish to thank three anonymous reviewers for their very helpful comments. YL and ZG were supported by the National Science Foundation of China (No. 11771104), Program for Chang Jiang Scholars and Innovative Research Team in University (IRT-16R16). LW was partially supported by a Discovery grant from the Natural Sciences and Engineering Research Council of Canada.

Conflict of interest

The authors declare that they have no competing interests.

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