

Spreading profiles of solutions to a free boundary problem for a reaction-diffusion equation*

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1 Introduction

In this article we will discuss some recent results by Kaneko-Matsuzawa-Yamada [11] on a free boundary problem for a reaction-diffusion equation.

We consider a free boundary problem for a reaction-diffusion equation given by

$$\begin{cases} u_t = u_{xx} + f(u), & t > 0, 0 < x < h(t), \\ u_x(t, 0) = 0, u(t, h(t)) = 0, & t > 0, \\ h'(t) = -\mu u_x(t, h(t)), & t > 0, \\ h(0) = h_0, u(0, x) = u_0(x), & 0 \leq x \leq h_0, \end{cases} \quad (1.1)$$

where μ and h_0 are positive constants, and the initial function u_0 satisfies

$$u_0 \in C^2([0, h_0]), \quad u_0 > 0 \text{ in } [0, h_0), \quad u'_0(0) = u_0(h_0) = 0 \text{ and } u'_0(h_0) < 0.$$

Moreover nonlinear function $f(u)$ is assumed to satisfy the following conditions:

$$\begin{cases} f(u) = 0 \text{ if and only if } u = 0, u_1^*, u_2^*, u_3^* \text{ with } 0 < u_1^* < u_2^* < u_3^*, \\ f'(0) > 0, f'(u_1^*) < 0, f'(u_2^*) > 0, f'(u_3^*) < 0 \text{ and} \\ \int_{u_1^*}^{u_3^*} f(u) du > 0. \end{cases} \quad (1.2)$$

The nonlinear term is called *positive bistable nonlinearity*. Different from the typical bistable nonlinearity, it has two positive stable equilibrium states u_1^*, u_3^* .

Problem (1.1) may be applied to model the spreading of new or invasive species in ecology. The spread of biological species is one of the central topic in mathematical ecology. Since Skellam's investigation (Skellam [18]), invasion phenomena have been widely studied by lots of researchers (see e.g. Shigesada-Kawasaki [17]). Nonlinearity (1.2) was especially introduced by Ludwig-Aronson-Weinberger [15] to model the population dynamics of spruce

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budworm in North America. The difference between previous works on invasion phenomena and problem (1.1) is that the problem is described as a free boundary problem, where $u(t, x)$ represents the population density of a species and free boundary $h(t)$ denotes the spreading front of one-dimensional habitat $(0, h(t))$. The dynamical behavior of the free boundary is also determined by Stefan condition $h'(t) = -\mu u_x(t, h(t))$. We consider a pair of solution $(u(t, x), h(t))$ to (1.1) to investigate the spread of new or invasive species.

This type of free boundary problem was first proposed by Du-Lin [2] when $f(u) = u(a - bu)$ for $a, b > 0$. They obtained the existence and uniqueness of global solutions and showed *spreading* and *vanishing* in large time behaviors of solutions. For any solution of their free boundary problem, either (i) or (ii) holds as $t \rightarrow \infty$:

- (i) *Spreading*: $\lim_{t \rightarrow \infty} h(t) = \infty$ and $\lim_{t \rightarrow \infty} u(t, x) = \frac{a}{b}$ locally uniformly in $\mathbb{R}$,
- (ii) *Vanishing*: $\lim_{t \rightarrow \infty} h(t) \leq \frac{\pi}{2\sqrt{a}}$ and $\lim_{t \rightarrow \infty} \sup_{0 \leq x \leq h(t)} |u(t, x)| = 0$.

After the work of Du-Lin [2], their results were extended by many researchers (cf. [3]–[4], [6]–[14]). We also refer to Mimura-Yamada-Yotsutani [16] a free boundary problem for a system of reaction-diffusion equations. It is seen that problem (1.1) has a unique classical solution $(u(t, x), h(t))$ satisfying

$$0 < u(t, x) \leq C_1 \text{ for } t > 0, 0 < x < h(t) \text{ and } 0 < h'(t) \leq \mu C_2 \text{ for } t > 0$$

for some constants $C_1, C_2 > 0$ when f is locally Lipschitz continuous in $[0, \infty)$, $f(0) = 0$ and $f(u) < 0$ for all large $u > 0$ (see Kaneko-Yamada [9]). Moreover Kawai-Yamada [12] studied problem (1.1) with positive bistable nonlinearity (1.2). They showed that exactly one of the followings occurs for any solution (u, h) as $t \rightarrow \infty$:

- (i) *Vanishing*: $\lim_{t \rightarrow \infty} h(t) \leq \frac{\pi}{2\sqrt{f'(0)}}$ and $\lim_{t \rightarrow \infty} \sup_{0 \leq x \leq h(t)} |u(t, x)| = 0$,
- (ii) *Small Spreading*: $\lim_{t \rightarrow \infty} h(t) = \infty$ and $\lim_{t \rightarrow \infty} u(t, x) = u_1^*$ locally uniformly in $\mathbb{R}$,
- (iii) *Big Spreading*: $\lim_{t \rightarrow \infty} h(t) = \infty$ and $\lim_{t \rightarrow \infty} u(t, x) = u_3^*$ locally uniformly in $\mathbb{R}$,
- (iv) *Transition*: $\lim_{t \rightarrow \infty} h(t) = \infty$ and $\lim_{t \rightarrow \infty} u(t, x) = V(x)$ locally uniformly in $\mathbb{R}$,

where $V(x)$ is a unique solution to

$$V'' + f(V) = 0 \text{ in } (0, \infty), V'(0) = 0 \text{ and } \lim_{x \rightarrow \infty} V(x) = u_1^*.$$

The main purpose of this article is to show the asymptotic profile of solutions as $t \rightarrow \infty$. Since small and big spreading mean local uniform convergence of $u(t, \cdot)$ in $\mathbb{R}$ (that is, uniform convergence in $[0, R]$ for any $R > 0$), they do

not give detailed information near the free boundary. It is known that, for typical type of f , the spreading speed and the asymptotic profiles of solutions near the spreading front are determined by the following semi-wave problem:

$$(SWP) \quad \begin{cases} q'' - cq' + f(q) = 0, & q(z) > 0 \quad \text{for } z > 0, \\ q(0) = 0, \quad \mu q'(0) = c, & \lim_{z \rightarrow \infty} q(z) = u^*, \end{cases}$$

where μ is given in (1.1) and u^* stands for a positive zero point of f . For solution (c^*, q^*) to (SWP), we call function q^* *semi-wave* and refer to c^* as *spreading speed*. When $u^* = u_1^*$ (corresponding to the small spreading case), there exist a unique solution pair $(c, q) = (c_S, q_S)$ to (SWP) and a constant $\hat{H} \in \mathbb{R}$ such that

$$\lim_{t \rightarrow \infty} (h(t) - c_S t) = \hat{H} \quad \text{and} \quad \lim_{t \rightarrow \infty} \sup_{0 \leq x \leq h(t)} |u(t, x) - q_S(h(t) - x)| = 0.$$

However the situation for $u^* = u_3^*$ (the big spreading case) is more complicated and it is divided into two cases: (Case A) there exists a unique solution pair to (SWP) for any $\mu > 0$, while (Case B) we can find some $\mu^* > 0$ such that (SWP) has a unique solution pair (c_B, q_B) to (SWP) for $\mu < \mu^*$ and no solutions for $\mu \geq \mu^*$. Moreover average speed is given by

$$\lim_{t \rightarrow \infty} \frac{h(t)}{t} = \begin{cases} c_B, & \text{if } \mu < \mu^*, \\ c_S, & \text{if } \mu \geq \mu^*. \end{cases}$$

If (SWP) with $u^* = u_3^*$ has a unique solution, it is possible to show that the asymptotic profile of u near the free boundary is determined by the semi-wave, that is,

$$\lim_{t \rightarrow \infty} (h(t) - c_B t) = H^* \quad \text{and} \quad \lim_{t \rightarrow \infty} \sup_{0 \leq x \leq h(t)} |u(t, x) - q_B(h(t) - x)| = 0$$

for some constant $H^* \in \mathbb{R}$. In the other case the asymptotic profile of solutions is not obtained by (SWP) with $u^* = u_3^*$. Then it was numerically observed that the solution to (1.1) can form a so called *propagating terrace* (see Figure 1). The notion of propagating terrace arise from Ducrot-Giletti-Matano [5] for a Cauchy problem of a reaction-diffusion equation. We are thus interested in such a terraced profile of solutions.

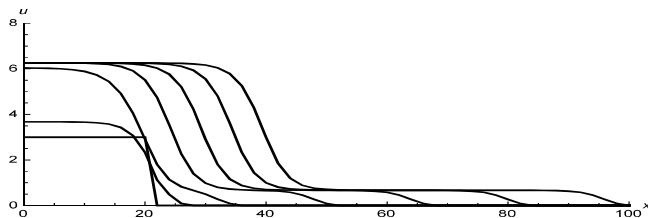


Figure 1 : Numerical example for terraced profile

This article is organized as follows: in Section 2 we prepare some notations and an assumption. Section 3 is devoted to main results concerning on the profile of propagating terrace and the proofs of the main results.

2 Notations and assumption (TW)

In this section we will prepare for main results. Let $c_S(\mu)$ and $c_B(\mu)$ be defined as in Section 1. Here μ is a given constant in (1.1) and we make it clear the dependence of the spreading speeds on μ .

We now prepare traveling waves to explain the relation with $c_S(\mu)$ and $c_B(\mu)$. One can regard positive bistable term $f(u)$ as the combination of $f|_{[0, u_1^*]}$ and $f|_{[u_2^*, u_3^*]}$, where $f|_{[a, b]}$ denotes the restriction of f onto $[a, b]$. Then we see $f|_{[0, u_1^*]}$ as monostable term and $f|_{[u_2^*, u_3^*]}$ as bistable one (see Figure 2), and get a traveling wave corresponding to each part in the following way.

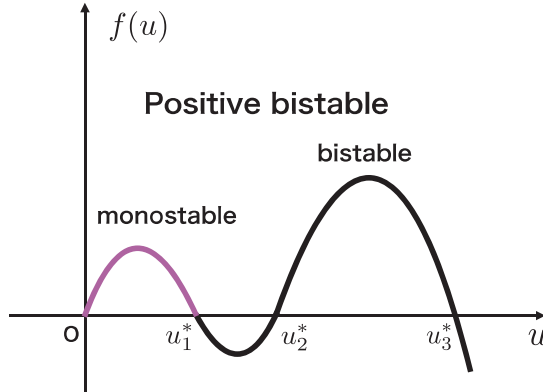


Figure 2 : Positive bistable term

Consider

$$\begin{cases} Q'' - cQ' + f(Q) = 0, & q(z) > 0 \quad \text{for } -\infty < z < \infty, \\ \lim_{z \rightarrow -\infty} Q(z) = u_1^*, & Q(0) = (u_1^* + u_3^*)/2, \quad \lim_{z \rightarrow \infty} Q(z) = u_3^* \end{cases} \quad (2.1)$$

and

$$\begin{cases} Q'' - cQ' + f(Q) = 0, & q(z) > 0 \quad \text{for } -\infty < z < \infty, \\ \lim_{z \rightarrow -\infty} Q(z) = 0, & Q(0) = u_1^*/2, \quad \lim_{z \rightarrow \infty} Q(z) = u_1^*. \end{cases} \quad (2.2)$$

It is well known that there exists a unique $c = c_1^B$ such that (2.1) has a unique (up to shift) solution $Q = Q_1^B(z)$ and that (2.2) has solutions for $|c| \geq c_0^S$ for a minimal speed $c_0^S > 0$.

To get the terraced profile we need an assumption. Recall Case B in Section 1; where (SWP) with $u^* = u_3^*$ has no solutions for large μ . Then $\lim_{t \rightarrow \infty} h(t)/t = c_S$. It is necessary to assume $c_1^B < c_0^S$ to deduce this estimate. By Kawai-Yamada [12] and Du-Lou [3], we find that semi-wave speeds $c_S(\mu), c_B(\mu)$ are increasing with respect to μ , and satisfy

$$c_S(\mu) < c_0^S, \quad c_B(\mu) < c_1^B$$

and

$$c_S(\mu) \rightarrow c_0^S \quad \text{as } \mu \rightarrow \infty, \quad c_S(\mu) \rightarrow 0 \quad \text{as } \mu \rightarrow 0.$$

If we assume $c_1^B < c_0^S$, then there exists $\mu^* > 0$ such that $c_S(\mu^*) = c_1^B$, and hence $c_S(\mu) > c_1^B$ for $\mu > \mu^*$ (see Figure 3). In the rest of the article we assume

$$(TW) \quad c_1^B < c_0^S \quad \text{and} \quad \mu > \mu^*.$$

Our strategy to get the terraced profile is to approximate the solution for $u \geq u_1^*$ by the traveling wave and for $u < u_1^*$ by the semi-wave (see Figure 4).

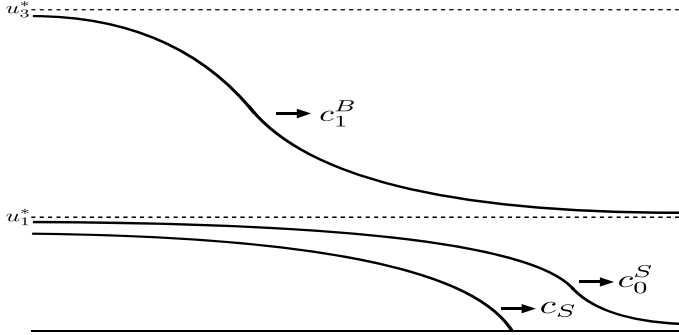


Figure 3 : Case $c_1^B < c_0^S$ and $\mu > \mu^*$

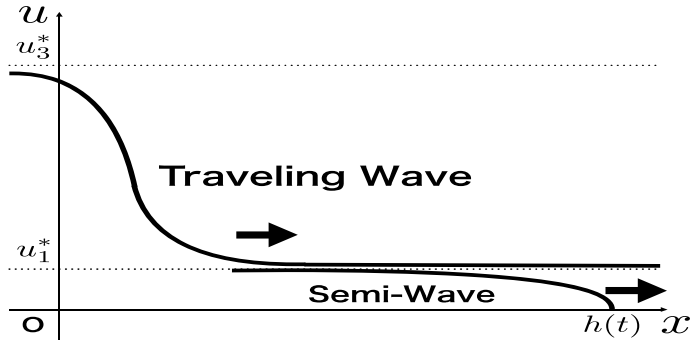


Figure 4 : Approximation by traveling wave and semi-wave

Finally we prepare a comparison principle which is useful to prove main results. A pair of functions $(\underline{u}, \underline{h})$ in the following lemma is called lower solution to (1.1). An upper solution is defined in a similar way.

Lemma 1. *Let $\underline{h} \in C^1([0, T])$ and $\underline{u} \in C(\Omega_1) \cap C^{1,2}(\Omega_1)$ with $\Omega_1 = \{(t, x) \in \mathbb{R}^2 \mid 0 \leq x \leq \underline{h}(t) \text{ for } 0 < t \leq T\}$ satisfy*

$$\begin{cases} \underline{u}_t \leq \underline{u}_{xx} + f(\underline{u}), & (t, x) \in \Omega_1, \\ \underline{u}_x(t, 0) \geq 0, \quad \underline{u}(t, \underline{h}(t)) = 0, & t \in (0, T], \\ \underline{h}'(t) \leq -\mu \underline{u}_x(t, \underline{h}(t)), & t \in (0, T]. \end{cases}$$

If $\underline{h}(0) \leq h_0$ and $\underline{u}(0, x) \leq u_0(x)$ in $[0, \underline{h}(0)]$, then

$$\underline{h}(t) \leq h(t) \text{ in } [0, T] \quad \text{and} \quad \underline{u}(t, x) \leq u(t, x) \text{ in } \overline{\Omega}_1.$$

3 Main results and proofs

3.1 Main results

We will see main results in this section. Let (u, h) be a solution to (1.1). We call (u, h) *big spreading solution* if and only if $u(t, x)$ and $h(t)$ satisfy

$$\lim_{t \rightarrow \infty} h(t) = \infty \quad \text{and} \quad \lim_{t \rightarrow \infty} u(t, x) = u_3^* \quad \text{locally uniformly in } \mathbb{R}.$$

The following result is concerned with rough estimates of the asymptotic profile of solutions.

Theorem 1 ([11]). *Assume (TW). Let (u, h) be any big spreading solution to (1.1). For any small $\varepsilon > 0$, there exist $M > 0$, $\delta > 0$ and $T > 0$ such that for $t \geq T$*

$$\sup_{x \in [0, (c_1^B - \varepsilon)t]} |u(t, x) - u_3^*| \leq M e^{-\delta t}, \quad (3.1)$$

$$\sup_{x \in [(c_1^B + \varepsilon)t, (c_S - \varepsilon)t]} |u(t, x) - u_1^*| \leq M e^{-\delta t}, \quad (3.2)$$

where c_1^B denotes the speed of traveling wave defined in Section 2 and c_S represents the speed of semi-wave defined in Section 1.

We will explain a terraced profile of big spreading solutions to (1.1).

Theorem 2 ([11]). *Assume (TW). Let (u, h) be any big spreading solution to (1.1) and let (c_S, q_S) be the solution to (SWP) with $u = u_1^*$. Then, for any $c \in (c_1^B, c_S)$, there exist $H_S, H_B \in \mathbb{R}$ such that*

$$\begin{aligned} \lim_{t \rightarrow \infty} (h(t) - c_S t - H_S) &= 0, \quad \lim_{t \rightarrow \infty} h'(t) = c_S, \\ \lim_{t \rightarrow \infty} \sup_{x \in [ct, h(t)]} |u(t, x) - q_S(h(t) - x)| &= 0 \quad \text{and} \\ \lim_{t \rightarrow \infty} \sup_{x \in [0, ct]} |u(t, x) - Q_1^B(c_1^B t + H_B - x)| &= 0, \end{aligned}$$

where Q_1^B is a unique solution to (2.1) with $c = c_1^B$.

3.2 Proof of Theorem 1

We first show (3.1). Let $U = U(t)$ be a solution of

$$\begin{cases} U_t = f(U), & t > 0, \\ U(0) = a > \max\{\|u_0\|_{C([0, h_0])}, u_3^*\}. \end{cases}$$

Then the standard comparison principle gives $u(t, x) \leq U(t)$ for $t > 0$, $0 < x < h(t)$. Moreover $U(t)$ is monotone decreasing with respect to t and converges to u_3^* as $t \rightarrow \infty$. From the linearization problem at $U = u_3^*$, we can choose positive constants T^*, δ and M such that

$$u(t, x) \leq u_3^* + M e^{-\delta t} \quad \text{for } t \geq T^*, \quad 0 \leq x \leq h(t).$$

Fix $c \in (0, c_1^B)$. Let $q_c = q_c(z)$ be a solution of $q_c'' - c q_c' + f(q_c) = 0$ such that $Q_c := q_c(0) < u_3^*$, $q_c'(0) = 0$, $q_c(-z_1) = 0$ and $q_c' > 0$ in $[-z_1, 0)$ for some constant $z_1 > 0$. Then we see $Q_c \rightarrow u_3^*$ as $c \rightarrow c_1^B$. Define

$$\underline{u}(t, x) = \begin{cases} Q_c, & 0 \leq x \leq ct, \\ q_c(ct - x), & ct \leq x \leq ct + z_1 \end{cases} \quad \text{and} \quad \underline{h}(t) = ct + z_1.$$

Letting c sufficiently close to c_1^B , we deduce from Lemma 1 that

$$\underline{h}(t - T_1) \leq h(t) \quad \text{for } t \geq T_2, \quad \underline{u}(t - T_1, x) \leq u(t, x) \quad \text{for } t > T_2, \quad 0 \leq x \leq \underline{h}(t - T_1)$$

for some constants T_1, T_2 with $T_1 < T_2$. In particular $u(t, x) \geq Q_c$ for $t \geq T_2$, $0 \leq x \leq c(t - T_1)$. Moreover, taking $c(< c_1^B)$ and T^* suitably large, we have

$$(c_1^B - \varepsilon)t \leq c(t - T_1) \quad \text{for } t \geq T^*.$$

Using the above estimate and $Q_c \rightarrow u_3^*$ as $c \rightarrow c_1^B$, one can choose suitable constant $T^*, M, \delta > 0$ satisfying

$$u(t, x) \geq u_3^* - M e^{-\delta t} \quad \text{for } t \geq T^*, \quad 0 \leq x \leq (c_1^B - \varepsilon)t.$$

These estimates show (3.1) (See Figure 5). We next prove (3.2). It is easy to check that

$$s(t) = c_S(t - T) + h_0, \quad w(t, x) = q_S(s(t) - x)$$

is a lower solution to (1.1) for $t \geq T, 0 \leq x \leq s(t)$. Note that there exist $C_0, \gamma > 0$ satisfying $q_S(z) \geq u_1^* - C_0 e^{-\gamma z}$ for $z \geq 0$. Then, for any $c \in (0, c_S)$, we obtain

$$u(t, x) \geq u_1^* - \tilde{M} e^{-\tilde{\delta} t} \quad t \geq \tilde{T}, \quad 0 \leq x \leq ct$$

with some constants $\tilde{T}, \tilde{M}, \tilde{\delta} > 0$. Let

$$\bar{u}(t, x) = Q_1^B(c_1^B(t - T_0) + X_0 + M_0\rho(e^{-\delta_0 T_0} - e^{-\delta_0 t}) - x) + M_0 e^{-\delta_0 t}$$

for positive constants T_0, X_0, M_0, ρ and δ_0 . Then, by choosing the constants suitably, the standard comparison principle proves $u(t, x) \leq \bar{u}(t, x)$ for $t \geq T_0, 0 \leq x \leq h(t)$. This estimate enables us to get, for any $c \in (c_1^B, c_S)$

$$u(t, x) \leq u_1^* + M_0 e^{-\delta_0 t} \quad t \geq T_0, \quad ct \leq x \leq h(t)$$

by adjusting the constants (see Figure 5). These estimates prove (3.2). $\square$

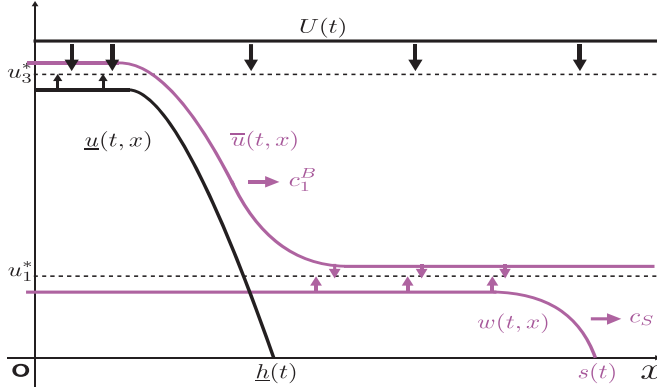


Figure 5 : Functions compared with solutions

3.3 Proof of Theorem 2

The spreading speed estimate and the convergence of u to semi-wave q_S are proved by a similar manner as in Du-Matsuzawa-Zhou [4] and Kaneko-Yamada [10] by zero number arguments and the comparison principle. Hence it remains to show the convergence to traveling wave Q_1^B . As in the proof of Theorem 1, we can construct upper and lower solutions and find some constants $H_0, H_1 \in \mathbb{R}$ and $T, M, \delta > 0$ such that

$$Q_1^B(c_1^B t + H_1 - x) - M e^{-\delta t} \leq u(t, x) \leq Q_1^B(c_1^B t + H_0 - x) + M e^{-\delta t}$$

for $t \geq T$, $0 \leq x \leq ct$ with $c \in (c_1^B, c_S)$. Define $v(t, z) = u(t, z + c_1^B t)$. Then it follows that

$$Q_1^B(H_1 - z) - Me^{-\delta t} \leq v(t, z) \leq Q_1^B(H_0 - z) + Me^{-\delta t}$$

for $t \geq T$, $-c_1^B t \leq z \leq (c - c_1^B)t$. By Berestycki-Hamel [1], $v(t, z)$ converges along subsequences $\{t_n\}$ to a traveling waves locally uniformly in $\mathbb{R}$, that is,

$$v(t_n, z) \rightarrow Q_1^B(H_B - z) \quad \text{locally uniformly in } \mathbb{R} \quad \text{as } n \rightarrow \infty$$

for some constant H_B . We can finally prove that H_B does not depend on the subsequences by constructing appropriate upper and lower solutions. The proof is complete. $\square$

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References

- [1] H. Berestycki and F. Hamel, *Generalized traveling waves for reaction-diffusion equations*, in “Perspective in Nonlinear Partial Differential Equations”, in honor of H. Brezis, Contemp. Math., Vol. 446, Amer. Math. Soc., Providence, RI, 2007, pp. 211-237.
- [2] Y. Du and Z. G. Lin, *Spreading-vanishing dichotomy in the diffusive logistic model with a free boundary*, SIAM J. Math. Anal., **42** (2010), pp. 377-405.
- [3] Y. Du and B. Lou, *Spreading and vanishing in nonlinear diffusion problems with free boundaries*, J. Eur. Math. Soc., **17** (2015), pp. 2673-2724.
- [4] Y. Du, H. Matsuzawa and M. Zhou, *Sharp estimate of the spreading speed determined by nonlinear free boundary problems*, SIAM J. Math. Anal., **46** (2014), pp. 375-396.
- [5] A. Ducrot, T. Giletti and H. Matano, *Existence and convergence to a propagating terrace in one-dimensional reaction-diffusion equations*, Trans. Amer. Math. Soc., **366** (2014), pp. 5541-5566.
- [6] J. S. Guo and C. H. Wu, *Dynamics for a two-species competition-diffusion model with two free boundaries*, Nonlinearity, **28** (2015), pp. 1-27.

- [7] J. S. Guo and C. H. Wu, *On a free boundary problem for a two-species weak competition system*, J. Dyn. Diff. Equat., **22** (2012), pp. 873-895.
- [8] Y. Kaneko, K. Oeda and Y. Yamada, *Remarks on spreading and vanishing for free boundary problems of some reaction-diffusion equations*, Funkcial. Ekvac., **57** (2014), pp. 449-465.
- [9] Y. Kaneko and Y. Yamada, *A free boundary problem for a reaction-diffusion equation appearing in ecology*, Adv. Math. Sci. Appl., **21** (2011), pp. 467-492.
- [10] Y. Kaneko and Y. Yamada, *Spreading speed and profiles of solutions to a free boundary problem with Dirichlet boundary conditions*, J. Math. Anal. Appl., **465** (2018), pp. 1159-1175.
- [11] Y. Kaneko, H. Matsuzawa and Y. Yamada, *Asymptotic profiles of solutions and propagating terrace for a free boundary problem of nonlinear diffusion equation with positive bistable nonlinearity*, preprint.
- [12] Y. Kawai and Y. Yamada, *Multiple spreading phenomena for a free boundary problem of a reaction-diffusion equation with a certain class of bistable nonlinearity*, J. Differential Equations, **261** (2016), pp. 538-572.
- [13] X. Liu and B. Lou, *Asymptotic behavior of solutions to diffusion problems with robin and free boundary conditions*, Math. Model. Nat. Phenom., **8** (2013), pp. 18-32.
- [14] X. Liu and B. Lou, *On a reaction-diffusion equation with Robin and free boundary conditions*, J. Differential Equations, **259** (2015), 423-453.
- [15] D. Ludwig, D.G. Aronson and H.F. Weinberger, *Spatial patterning of the spruce budworm*, J. Math. Biol., **8** (1979), pp. 217-258.
- [16] M. Mimura, Y. Yamada and S. Yotsutani, *A free boundary problem in ecology*, Japan J. Appl. Math., **2** (1985), pp. 151-186.
- [17] N. Shigesada and K. Kawasaki, *Biological invasions: Theory and Practice*, Oxford Series in Ecology and Evolution, Oxford Univ. Press, 1997.
- [18] J. G. Skellam, *Random dispersal in theoretical populations*, Biometrika, **38** (1951), pp. 196-218.