

Mathematical study on sharing metabolism

By

Shinji NAKAOKA* and Yasuhiro TAKEUCHI**

Abstract

We study a mathematical model describing the population dynamics of microbial species competing for a family of organic compounds. Our study is based on some experimental study for microbial consortium which consists of two species sharing the metabolism of organic compounds. Our study suggests that sharing metabolism can facilitate the coexistence of two species provided that the sharing is mutualistic in a sense that one species cannot be activated without the other.

§ 1. Introduction

Resource competition is common in nature ([4], [9], [17]). Different species living in the same field are often in face of competition for available resources. The difference of resource availability among competitively interacting species often has a great impact on the population growth and determines the fate of species. The competitive exclusion principle (hereafter we use the abbreviation “CEP”) predicts that the number of species competing for the several available resources cannot exceed the number of available resources in steady state. Several basic mathematical models describing the resource competition for the limiting resources have been proposed and the consequences agree with the CEP ([2], [11]). Of course, this prediction does not explain correctly what is observed in nature. This paradox has fascinated to propose driving factors which facilitate the coexistence of species being in face of resource competition as opposed to the CEP. It is important not only to propose biologically feasible mechanisms underlying

2000 Mathematics Subject Classification(s): 2000 Mathematics Subject Classification(s):37N25, 62P10, 92B05

Key Words: microbial consortium; sharing metabolism; extracellular metabolism; mathematical model; population dynamics; chemostat-type equations; resource competition; mutual coexistence; bioremediation;

*Aihara Complexity Modelling Project, ERATO, JST, Komaba Open Laboratory, The University of Tokyo, 153-8505, Japan.

**Graduate school of Science and Engineering, Shizuoka University, 432-8561, Japan.

species coexistence, but also to extend a framework of the mathematical theory on resource competition.

It is often the case with microbial species that the difference of metabolism results in the difference of resource availability. Microbiological metabolism is one of the most important studies in microbiology. There are well known evidences that some microorganism, for example, *Methylocystis* sp. *M* is capable of degrading trichloroethylene (TCE), which is commonly used as an industrial solvent for a variety of organic materials. It has been revealed that the exposure to TCE is supposed to bring harmful effects on human health so that the elimination of TCE accumulated in soil or groundwater is an important environmental issue on health and environmental sciences. The elimination of TCE can be mediated by the activities of microorganisms which are capable of degrading TCE. It is well known that the microbiological degradation of TCE is primarily achieved by cometabolism. Cometabolism is defined as a biological transformation of an organic compound which is incapable of using as a resource for microorganisms, but it can lead to produce another organic compound or by-product which can be a food source for microorganisms. Recently, theoretical and mathematical studies on microbiological metabolism seem to be getting major (see for example, [6], [12]).

The degradation of organic compounds is not necessarily carried out by one species. It can happen that more than two species are involved to metabolize some organic compound. These microorganisms form a microbial consortium in which different species complementarily share the part of metabolic pathway in order to maintain their community. The understandings for the metabolism of some organic compound within a microbial consortium are necessary to develop bioremediation technology. Bioremediation technology enables us to degrade organic compounds in soil or groundwater which would be harmful to human health.

Let us briefly review some experimental study on microbial degradation of some organic compound in an experimental environment called *microcosm*. Fenitrothion (hereafter we call it substance 0) is a phosphorganic pesticide which is contained not only in agricultural pesticides but also in domestic insecticides. In the experimental study, a fenitrothion degrading bacterium *Spingomonas* species TFEE0205 (species 1) was isolated which possesses an ability to metabolize fenitrothion to an intermediate substance 3-methyl-4-nitrophenol (substance 1) via extracellular enzyme synthesized by TFEE 0205. A bacterium *Burkholderia* species 3M4N01 (species 2) was also isolated which possesses an ability to metabolize 3-methyl-4-nitrophenol (substance 1) to the next intermediate substance methylhydroquinone (substance 2). It was confirmed that species 1 is incapable of metabolizing substance 1 to substance 2, while species 2 is incapable of metabolizing substance 0 (fenitrothion) to substance 1. Thus it was suggested that

these two species form a consortium and get an ability to degrade fenitrothion via mutualistic manner. This experimental study is im preparation to submit. Another similar studies can be refereed in [1], [3], [13], [14].

In this paper, we consider the following system of differential equations

$$(1.1) \quad \begin{cases} S'_0 = \lambda - d_0 S_0 - \beta S_0 x_1, \\ S'_1 = -d_1 S_1 + \beta S_0 x_1 - f_{12}(S_1) \frac{x_2}{\eta_2}, \\ S'_2 = -d_2 S_2 + \gamma f_{12}(S_1) \frac{x_2}{\eta_2} - f_{21}(S_2) \frac{x_1}{\eta_1} - f_{22}(S_2) \frac{x_2}{\eta_2}, \\ x'_1 = x_1 (f_{21}(S_2) - \mu_1), \\ x'_2 = x_2 ((1 - \gamma) f_{12}(S_1) + f_{22}(S_2) - \mu_2) \end{cases}$$

with non-negative initial condition

$$(I) \quad (S_0(0), S_1(0), S_2(0), x_1(0), x_2(0)) \in \mathbb{R}_+^5.$$

Here S_0 , S_1 and S_2 denote the concentrations of substance 0 (fenitrothion), substance 1 (3-methyl-4-nitrophenol) and substance 2 (methylhydroquinone), respectively. Let x_1 and x_2 denote the concentrations of species 1 (TFEE0205) and species 2 (3M4N01), respectively. λ is a constant input rate of substance 0 to the microcosm. The respective decay rates of substance 0, 1 and 2 are given by d_0 , d_1 and d_2 . Parameters μ_1 and μ_2 represent the inactivation (including death and quiescence etc.) rates of species 1 and 2, respectively. β measures the degree of fenitrothion metabolism by the extracellular digestion of species 1. Large β represents the strong effect of extracellular metabolism, while small β represents the weak effect of extracellular metabolism. γ represents the fraction of transformation which takes a value between 0 and 1. In this context, the term “transformation” indicates that 3-methyl-4-nitrophenol is metabolized by species 2 but it is not dissimilated by species 2. Hence the term $\gamma f_{12}(S_1) \frac{x_2}{\eta_2}$ represents the amount of remained 3-methyl-4-nitrophenol substance in the microcosm. Since species 1 can feed substance 2, the term $f_{21}(S_2)$ represents a functional response of species 1 to substance 2. Typically, it is assumed to take the form of Monod-type (or Michaelis-Menten type which is equivalent to Monod-type in the equation):

$$(1.2) \quad f_{ij}(S_i) := \frac{m_{ij} S_i}{a_{ij} + S_i},$$

where m_{ij} denotes the maximum growth rate of species j by feeding substance i . a_{ij} is called a half-saturation constant. In this paper, we assume that $f_{ij}(S_i)$ is monotone increasing and bounded function of S_i . Moreover $f_{ij}(0) = 0$. We will fix the form of functional responses f_{12} , f_{21} and f_{22} to Monod-type whenever implementing numerical simulation and continuation. η_1 and η_2 represent the constant conversion rate of nutrient

to microorganism species 1 and 2, respectively. η_1 and η_2 are referred as yield constant (see [11]). Here we assumed that the respective conversion rates for substance 1 and 2 are same. We can show that the uniqueness and nonnegativeness of solutions are fulfilled (see for example, [16]). Moreover, system (1.1) with nonnegative initial condition (I) is dissipative (for the definition of dissipativeness, see [5]). To prove the dissipativeness, we can apply the similar method developed in [11, Chapter 2] so that the proof is omitted.

Note that two species are exploitatively competing for the common resource S_2 . The classical theory of the chemostat predicts that two species exploitatively competing for one common resource result in the competitive exclusion [11, Chapter 1, 2]. In other words, only one species which is superior to the exploitation of the common resource can survive. The mathematical definition of the competitive exclusion is nonexistence of stable interior equilibrium point of the system. If $\gamma = 1$, then the fourth and fifth equations of system (1.1) are reduced to

$$(1.3) \quad \begin{cases} x'_1 = x_1 (f_{21}(S_2) - \mu_1), \\ x'_2 = x_2 (f_{22}(S_2) - \mu_2). \end{cases}$$

It immediately follows from (1.3) that there is generically no interior equilibrium of system (1.1). More precisely, the interior equilibrium of system (1.3) exists only if

$$(1.4) \quad S_2^* = f_{21}^{-1}(\mu_1) = f_{22}^{-1}(\mu_2).$$

Condition (1.4) holds only for a special case. Hence generically, we do not expect to have an interior equilibrium of system (1.1) if $\gamma = 1$. This implies that two species cannot coexist in steady state, which reflects the competitive exclusion principle. However, now we consider the metabolism of pre-metabolized substances, substance 0 and 1. Hence the introduction of stage-structure in nutrient along the metabolic pathway of microorganisms can mediate the coexistence of two species against the competitive exclusion principle.

The purpose of this paper is to elucidate how sharing metabolism affects on the population dynamics of two species. We investigate conditions under which two species can stably coexist by steady-state analysis, numerical simulations and numerical continuation analysis. In the next section, we derive a limiting system of system (1.1). In Section 3, we derive conditions for the existence of interior equilibrium points of the limiting system of (1.1). In Section 4, we implement numerical simulations to examine whether two species can coexist by changing the value of γ . In Section 5, we implement numerical continuation methods by using CONTENT ([7], [8]) in order to investigate how equilibrium curves depend on the parameters β and γ . In the final section, we discuss our results in the biological context.

§ 2. Preliminaries

To obtain some analytical results, we apply a theory on asymptotically autonomous systems to our system. It allows us to study qualitative properties of the dynamical system on a restricted lower dimensional limiting system (2.3) instead of analyzing the original system (1.1). We introduce new variables, parameters and functions by

$$(2.1) \quad \begin{aligned} \bar{t} &= d_0 t, \quad \bar{S}_i = \frac{d_0}{\lambda} S_i \quad (i = 0, 1, 2), \quad \bar{x}_j = \frac{d_0}{\lambda \eta_j} x_j, \quad \bar{d}_j = \frac{d_j}{d_0}, \quad \bar{\mu}_j = \frac{\mu_j}{d_0} \quad (j = 1, 2), \\ \bar{\beta} &= \frac{\eta_1 \lambda}{d_0^2} \beta, \quad \bar{f}_{ij}(\bar{S}_i) = \frac{1}{d_0} f_{ij} \left(\frac{\lambda}{d_0} \bar{S}_i \right) \quad (i, j = 1, 2) \end{aligned}$$

Then we obtain that

$$(2.2) \quad \begin{cases} S'_0 = 1 - S_0 - \beta S_0 x_1, \\ S'_1 = -d_1 S_1 + \beta S_0 x_1 - f_{12}(S_1) x_2, \\ S'_2 = -d_2 S_2 + \gamma f_{12}(S_1) x_2 - f_{21}(S_2) x_1 - f_{22}(S_2) x_2, \\ x'_1 = x_1 (f_{21}(S_2) - \mu_1), \\ x'_2 = x_2 ((1 - \gamma) f_{12}(S_1) + f_{22}(S_2) - \mu_2), \end{cases}$$

where we abused to write “-” for all variables, parameters and functions on which we should have written. If $d_1 = d_2 = \mu_1 = \mu_2 = 1$, then the new variable $\Sigma := 1 - S_0 - S_1 - S_2 - x_1 - x_2$ satisfies the scalar linear differential equation $\Sigma' = -\Sigma(t)$. In (2.2), letting $S_0 = 1 - S_1 - S_2 - x_1 - x_2$ yields the following equations

$$(2.3) \quad \begin{cases} S'_1 = -S_1 + \beta(1 - S_1 - S_2 - x_1 - x_2) x_1 - f_{12}(S_1) x_2, \\ S'_2 = -S_2 + \gamma f_{12}(S_1) x_2 - f_{21}(S_2) x_1 - f_{22}(S_2) x_2, \\ x'_1 = x_1 (f_{21}(S_2) - 1), \\ x'_2 = x_2 ((1 - \gamma) f_{12}(S_1) + f_{22}(S_2) - 1). \end{cases}$$

For the biological relevance, we should restrict ourselves to take an initial point within the following region Ω :

$$\Omega = \{(S_1, S_2, x_1, x_2) : S_1 \geq 0, S_2 \geq 0, x_1 \geq 0, x_2 \geq 0, 0 \leq S_1 + S_2 + x_1 + x_2 \leq 1\}.$$

From

$$\lim_{t \rightarrow \infty} (S_0(t) + S_1(t) + S_2(t) + x_1(t) + x_2(t)) = 1,$$

one can conclude that omega limit set of the system (2.2) must lie in Ω , and trajectories on the omega limit set must satisfy (2.3). We can show that Ω is positively invariant. By virtue of a theory on asymptotic autonomous systems developed by Murkus [10] and Thieme [15] (also see the appendix F in [11]), we simply choose initial conditions in the

restricted region Ω and are allowed to eliminate one variable S_0 from the system (1.1). Of course, it is necessary to show that several assumptions must be fulfilled. Although it is still remained to check assumptions analytically, as long as we implement numerical simulations, all conditions are fulfilled. Throughout the remainder of this paper, we study a continuous dynamical system defined by the solution of system (2.3) starting with the initial point in Ω .

§ 3. Interior equilibrium points

We start to solve equilibrium points of (2.3). We consider

$$(3.1) \quad \begin{cases} -S_1 + \beta(1 - S_1 - S_2 - x_1 - x_2)x_1 - f_{12}(S_1)x_2 = 0, \\ -S_2 + \gamma f_{12}(S_1)x_2 - f_{21}(S_2)x_1 - f_{22}(S_2)x_2 = 0, \\ x_1(f_{21}(S_2) - 1) = 0, \\ x_2((1 - \gamma)f_{12}(S_1) + f_{22}(S_2) - 1) = 0. \end{cases}$$

Note that $x_1 = 0$ if and only if $x_2 = 0$. Moreover $S_1 = S_2 = 0$ if and only if $x_1 = x_2 = 0$. Let $E_0 := (0, 0, 0, 0)$ denote the trivial equilibrium point of system (2.3). The characteristic equation defined for the Jacobi matrix associated with the linearized equations for system (2.3) around E_0 is given by $(z + 1)^4 = 0$. Hence the trivial equilibrium is always locally asymptotically stable.

Let us investigate conditions under which positive equilibrium points of system (2.3) exist. For biological relevances, we impose that $x_1 > 0$ and $x_2 > 0$. It follows from the third equation of (3.1) that $f_{21}(S_2) - 1 = 0$. Since f_{21} is monotonically increasing (and bounded if necessary), there exists a positive value S_2^* which is a solution of $f_{21}(S_2) - 1 = 0$ if $\lim_{S \rightarrow \infty} f_{21}(S) > 1$. Similarly, there exists a positive value S_1^* which is a solution of $(1 - \gamma)f_{12}(S_1) + f_{22}(S_2^*) - 1 = 0$ if $1 - f_{22}(S_2^*) > 0$ and $\lim_{S \rightarrow \infty} f_{12}(S) > (1 - f_{22}(S_2^*))/(1 - \gamma)$. The first equation of (3.1) can be rewritten as

$$(3.2) \quad f_{12}(S_1^*)x_2 = \beta(1 - S_1^* - S_2^* - x_1 - x_2)x_1 - S_1^*.$$

$\beta(1 - S_1^* - S_2^* - x_1 - x_2) - S_1^*$ should be positive because now we impose that $x_2 > 0$. It follows from the third and fourth equations of (3.1) that

$$(3.3) \quad \gamma f_{12}(S_1^*) - f_{22}(S_2^*) = f_{12}(S_1^*) - 1.$$

It follows from the second equation of (3.1) and (3.3) that

$$(3.4) \quad x_1 = (f_{12}(S_1^*) - 1)x_2 - S_2^*,$$

where we used $f_{21}(S_2^*) = 1$. $f_{12}(S_1^*) - 1$ should be positive because now we impose that $x_1 > 0$. By (3.3), the lowest value of γ to ensure the existence of interior equilibrium

points must satisfy

$$(3.5) \quad \gamma > \frac{f_{22}(S_2^*)}{f_{12}(S_1^*)}.$$

(3.4) is equivalent to

$$(3.6) \quad S_2^* + x_1 + x_2 = f_{12}(S_1^*)x_2.$$

Adding all equations in (3.1) gives

$$(3.7) \quad S_1^* + S_2^* + x_1 + x_2 = \beta(1 - S_1^* - S_2^* - x_1 - x_2)x_1.$$

Substituting (3.4) and (3.6) into (3.7) gives the following equation with respect to x_2 :

$$(3.8) \quad \beta(1 - S_1^* - f_{12}(S_1^*)x_2) = \frac{S_1^* + f_{12}(S_1^*)x_2}{(f_{12}(S_1^*) - 1)x_2 - S_2^*}.$$

(3.8) is equivalent to the following quadratic equation:

$$(3.9) \quad c_0x_2^2 + c_1x_2 + c_2 = 0,$$

where

$$\begin{aligned} c_0 &= \beta f_{12}(S_1^*)(f_{12}(S_1^*) - 1) =: \alpha_{00}\beta, \\ c_1 &= f_{12}(S_1^*) - \beta\{S_2^*f_{12}(S_1^*) + (1 - S_1^*)(f_{12}(S_1^*) - 1)\} =: -\alpha_{11}\beta + \alpha_{10}, \\ c_2 &= \beta S_2^*(1 - S_1^*) + S_1^* =: \alpha_{21}\beta + \alpha_{20}. \end{aligned}$$

c_0 and c_2 are always positive. Thus there are two positive real roots of (3.9) if and only if $c_1 < 0$ and $c_1^2 - 4c_0c_2 > 0$. $c_1 < 0$ if and only if $\beta > \frac{\alpha_{10}}{\alpha_{11}}$.

$$c_1^2 - 4c_0c_2 = (\alpha_{11}^2 - 4\alpha_{00}\alpha_{21})\beta^2 - 2(\alpha_{10}\alpha_{11} + 2\alpha_{00}\alpha_{20})\beta + \alpha_{10}^2.$$

The coefficient of β^2 above is calculated as

$$\alpha_{11}^2 - 4\alpha_{00}\alpha_{21} = \{S_2^*f_{12}(S_1^*) - (1 - S_1^*)(f_{12}(S_1^*) - 1)\}^2 \geq 0.$$

Except for the special case that $\alpha_{11}^2 = 4\alpha_{00}\alpha_{21}$, $c_1^2 - 4c_0c_2 > 0$ for sufficiently large β . If $\alpha_{11}^2 = 4\alpha_{00}\alpha_{21}$, then the condition $c_1 < 0$ yields that

$$c_1^2 - 4c_0c_2 < -\alpha_{10}^2 - \alpha_{00}\alpha_{20}\beta < 0.$$

Hence there are no positive real roots of (3.9). In biological point of view, this result indicates that sufficiently large degradation of fenitrothion by extracellular enzyme is necessary for mediating the coexistence of two species.

§ 4. Numerical simulations

In the previous section, we showed that there exist two interior equilibrium points if β is sufficiently large. In this section, we implement numerical simulations to investigate the stability of two interior equilibrium points. Recall that there is always a locally stable equilibrium point $E_0 = (0, 0, 0, 0)$ which would be appropriately called *degradation-free* equilibrium. On the other hand, if there exists a stable interior equilibrium, it will be appropriate to call *degradation* equilibrium. In this and the following sections, we fix parameters m_{ij} and a_{ij} as

$$(4.1) \quad m_{12} = 5, m_{21} = 3, m_{22} = 8, a_{12} = 0.2, a_{21} = 0.05, a_{22} = 0.5.$$

Thus, two parameters β and γ are varied. In this section, we also fix the value of β as $\beta = 10$ and show four figures in each of which a set of solutions starting at different initial points is shown on x_1x_2 -plane. We always fix initial values for S_1 and S_2 as $S_1(0) = S_2(0) = 0.05$. Since we restrict to take initial conditions in the region Ω , initial points for x_1 and x_2 should be taken in the triangle region formed by x_1 -axis, x_2 -axis and the line $x_1 + x_2 = 0.9$. Three different values of γ are chosen to investigate the asymptotic behavior of the solutions of system (2.3). Figure 1 illustrates a set of orbits for $\gamma = 0.55$. For this parameter setting, we confirmed that there are no roots of the quadratic equation (3.9). Hence there are not interior equilibrium points. All orbits tend to the degradation-free equilibrium. Next, we increased the value of γ from 0.55 to 0.60. In this case, we can observe that only three orbits tend to the degradation-free equilibrium, while the other orbits tend to the degradation equilibrium (blue, filled circle) (see Figure 2). The region is divided into two parts; Solutions starting from one subregion tend to the degradation-free equilibrium, while solutions starting from another subregion tend to the degradation equilibrium. On Figure 2, a stable manifold of the saddle-type interior equilibrium point (red filled circle) divides the region. As changing the value of γ , the occurrence of saddle-node bifurcation is expected. This expectation is examined in the next section by numerical continuation methods. We further changed γ from 0.60 to 0.80. On Figure 3, no qualitative change from Figure 2 is observed. Finally, we changed γ from 0.80 to 0.82. In this case, we again observed the same situation as Figure 1. All solutions tend to the degradation-free equilibrium. We also confirmed that there are no positive roots of the quadratic equation (3.9) again. Consequently, these figures suggest that there are two threshold values of γ by which dynamical consequences are classified into two cases: (i) convergence to the degradation-free equilibrium, or (ii) bistability between the degradation-free and the degradation equilibrium points.

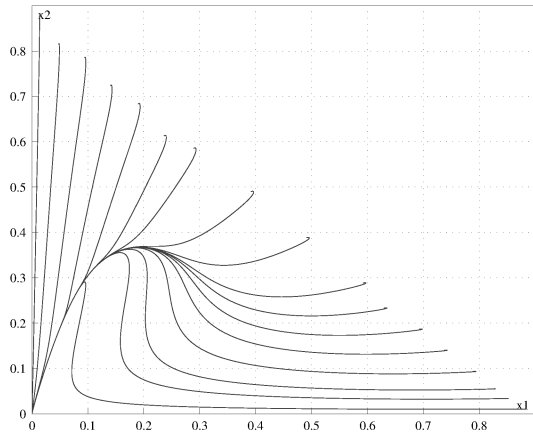


Figure 1. $\gamma = 0.55$: Degradation-free

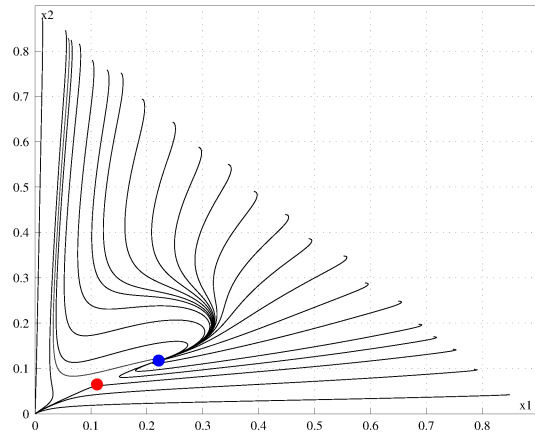


Figure 3. $\gamma = 0.8$: Degradation

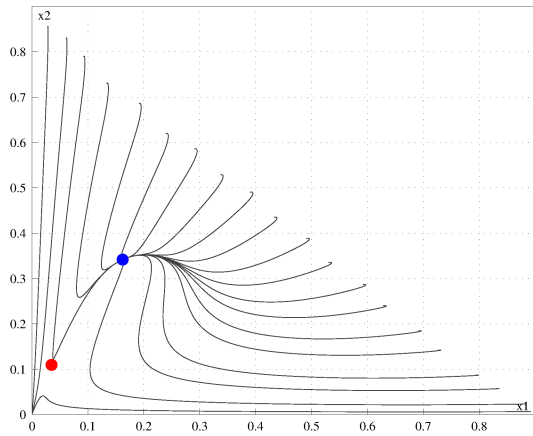


Figure 2. $\gamma = 0.60$: Degradation

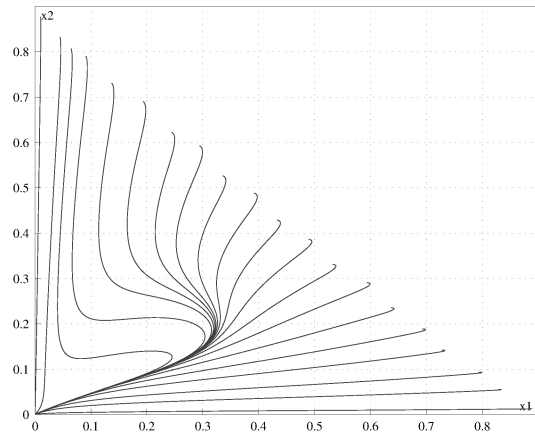


Figure 4. $\gamma = 0.82$: Degradation-free

§ 5. Numerical continuation analysis

In this section, we implement numerical continuation methods by using CONTENT in order to examine how equilibrium curves depend on the parameters β . γ is fixed at 0.8. We shall consider two situations according to the value of β . As we stated above, β measures the degree of fenitrothion metabolism by the extracellular metabolism of species 1.

§ 5.1. Weak extracellular metabolism: $\beta = 6.2$

We study the case where $\beta = 6.2$. Figures 5 and 6 illustrate equilibrium curves of x_1 and x_2 with respect to the parameter γ , respectively. In each Figure, we observe two **LP** points. Here, LP is an abbreviation of Limit Point. Thus the occurrence of the limit point, or saddle-node bifurcation, is confirmed by numerical continuation methods. Numerical computations suggest that the upper curve consists of stable-node equilibrium points (degradation equilibrium), while the lower curve consists of saddle equilibrium points. Note that saddle-node bifurcation occurs twice as γ changes from 0 to 1. At the left side of limit points in Figures 5 and 6, the critical value of γ is approximately given by $\gamma_1^* := 0.6792$. The equilibrium point is approximately given by $(0.126, 0.025, 0.117, 0.153)$. At the right side of limit point, the critical value of γ is approximately given by $\gamma_2^* := 0.7368$. The equilibrium point is $(0.178, 0.025, 0.143, 0.1245)$. We can see that the equilibrium curves form a closed curve. Let us measure the magnitude of extracellular metabolism by $\delta := \gamma_2^* - \gamma_1^*$. In this case, $\delta = 0.0576$.

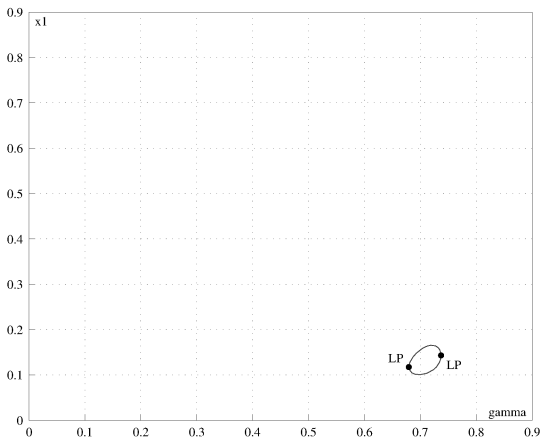


Figure 5. $\beta = 6.2$: γx_1 -plane

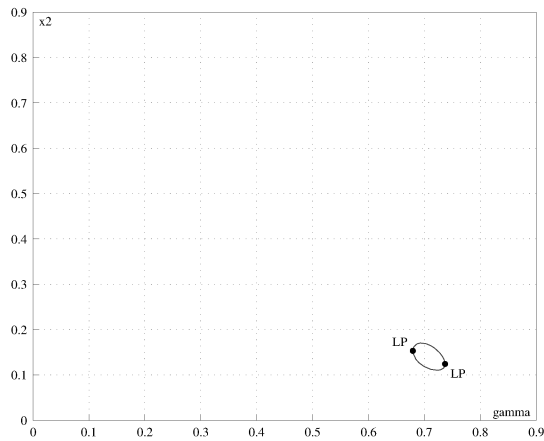


Figure 6. $\beta = 6.2$: γx_2 -plane

§ 5.2. Strong extracellular metabolism: $\beta = 40$

We study the case where $\beta = 40$. Figures 7 and 8 illustrate equilibrium curves of x_1 and x_2 with respect to the parameter γ , respectively. In this case, we also confirmed

the occurrence of the saddle-node bifurcation twice. At the left side of limit point in Figures 7 and 8, the critical value of γ is approximately given by $\gamma_1^* := 0.4507$. The equilibrium point is approximately given by $(0.058, 0.025, 0.028, 0.418)$. At the right side of limit point, the critical value of γ is approximately given by $\gamma_2^* := 0.8370$. The equilibrium point is $(0.632, 0.025, 0.111, 0.0486)$. We can also see that equilibrium curves form a closed curve. In this case, $\delta = 0.3863$. Compared Figures 5 and 6 with Figures 7 and 8, we can find that the range of region on which two interior equilibrium points exist becomes wider as β is increased from 6.2 to 40. This finding suggests that strong extracellular metabolism can facilitate the coexistence of two species.

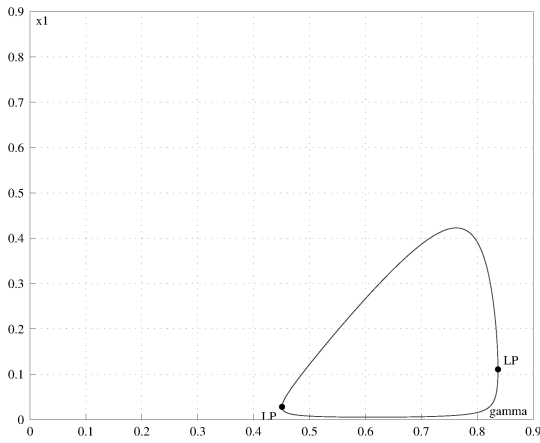


Figure 7. $\beta = 40$: γx_1 -plane

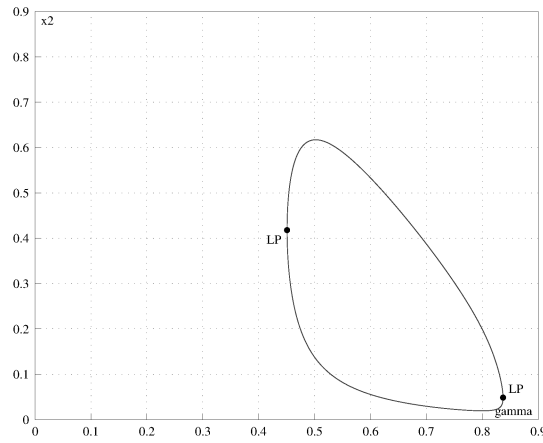


Figure 8. $\beta = 40$: γx_2 -plane

§ 6. Discussion

We studied a model for the population dynamics of two microbial species which are competing for the same family of organic compounds. This study was motivated by some experimental study on the microbiological degradation of an agricultural pesticide, fenitrothion. Two microorganisms were isolated and identified. They are capable of degrading fenitrothion in a mutualistic manner. Interestingly, these two microorganisms are incapable of degrading fenitrothion without the other. They are destined to alive together by owing to each other. Mathematical studies on the population dynamics describing phenomenon observed in the experiment revealed that there are two possible outcomes; (i) fenitrothion is not degraded and remains in the environment, or (ii) fenitrothion can be successfully degraded by two species. Notably, the degradation depends on initial conditions. There are two threshold values of γ by which the degradation is determined to be successful or to be failed. Another important finding is that the degree of extracellular metabolism by species 1 (represented by the parameter β) is

crucial to mediate and facilitate the degradation. Interestingly, in our study the competitive exclusion principle is not observed in generic situation. In this paper, we just implemented numerical simulations and continuations. Further mathematical analysis will be necessary to understand the structure which may be expected to become a basis to explain how so many microbial species can coexist even though they are in resource competition. Also, analytical and numerical investigations for the original system (1.1) are expected to study. These are left to our future work.

References

- [1] J.L. Alonso and J. Carrasco, Fenitrothion and 3-methyl-4-nitrophenol degradation by two bacteria in natural waters under laboratory conditions, *J. Environ. Sci. Health. Part A-Environ. Sci. Eng. Toxic. Hazard. Subst. Control* **32**, (1997) 799–812.
- [2] R. A. Armstrong and R. McGehee, Competitive exclusion, *Am. Nat.* **115** (1980), 151–170.
- [3] W. Dejonhe, E.M. Top, Synergetic degradation of linuron by a bacterial consortium and isolation of a single linuron-degrading *Variovorax* strain, *Appl. Environ. Microbiol.* **69** vol. 3 (2003), 1532–41.
- [4] J.P. Grover, “Resource Competition”, Population and Community Biology Series, vol. 19, Chapman and Hall, New York, 1997.
- [5] J. Hale, “Asymptotic Behavior of Dissipative Systems”. Providence, RI: American Mathematical Society. 1988.
- [6] J. Heßeler, J.K. Schmidt, U. Reichl and D. Flockerzi, Coexistence in the chemostat as a result of metabolic by-products, *J. Math. Biol.* **53** (2006), 556–584.
- [7] Y.A. Kuznetsov, Elements of Applied Bifurcation Theory 2nd edition, Springer New York (1998).
- [8] Y.A. Kuznetsov and V.V. Levitin, ”CONTENT: A multiplatform environment for continuation and bifurcation analysis of dynamical systems” (software under development) Centrum voor Wiskunde en Informatica, Kruislaan 413, 1098 SJ Amsterdam, The Netherlands (1997)
- [9] W.W. Murdoch, C.J. Briggs and R.M. Nisbet, “Consumer-Resource Dynamics”, Princeton University Press, Princeton, NJ, 2003.
- [10] L. Markus, “Asymptotically autonomous differential systems”, in *Contributions to the Theory of Nonlinear oscillation*, vol. 3. Princeton, NJ: Princeton University Press, pp. 17–29.
- [11] H. L. Smith and P. Waltman, “The Theory of the Chemostat”, Cambridge University Press, Cambridge, 1995.
- [12] R.W. Sterner and J.J. Elser, “Ecological Stoichiometry”, Princeton University Press, Princeton, NJ, 2003.
- [13] S.R. Sørensen, Z. Ronen and J. Aamand, Isolation from agricultural soil and characterization of a *Sphingomonas* sp. able to mineralize the phenylurea herbicide isoproturon, *Appl. Environ. Microbiol.* **67** vol. 12 (2001), 5403–09.
- [14] M.D. Souza, L.P. Wackett, Molecular basis of a bacterial consortium: interspecies catabolism of atrazine, *Appl. Environ. Microbiol.* **64** vol. 1 (1998), 178–84.
- [15] H. R. Thieme, Convergence results and a Poincaré-Bendixson trichotomy for asymptotically autonomous differential equations, *J. Math. Biol.*, **30** (1992), 755–763.

- [16] H.R. Thieme, “Mathematics in Population Biology”, Princeton University Press, 2003.
- [17] D. Tilman, “Resource Competition and Community Structure”, Princeton University Press, Princeton, NJ, 1982.