Konuralp Journal of Mathematics
Volume 4 No. 1 pp. 185–192 (2016) ©KJM

ON THE CODIMENSION-TWO AND -THREE BIFURCATIONS OF A FOOD WEB OF FOUR SPECIES

HSIU-CHUAN WEI, JENN-TSANN LIN, SHIN-FENG HWANG, AND YUH-YIH CHEN

Abstract. This paper is concerned with codimension-two and -three bifurcations of a food web containing a bottom prey X, two competing predators Y and Z on X, and a super predator W only on Y. Parameter conditions for a part of codimension-two bifurcations and a codimension-three bifurcation are derived. Three-parameter bifurcation diagrams are computed using an adaptive grid method to locate the bifurcations determined by the eigenvalues of equilibria.

1. Introduction

Mathematical modeling is a promising tool to analyze, predict, and control biological systems. Many mathematical models of biological systems use nonlinear dynamical systems. In this paper, we study bifurcations of a food web of four species considered in [5, 6]. The food web includes a bottom prey X, two predators Y and Z on X, and a super-predator W only on Y. The predators Y and Z have no direct competition. However, they have competition from consuming the same resource X. The dimensional model is as follows:

$$\frac{dX}{d\tau} = rX\left(1-\frac{X}{K}\right)-\frac{p_1X}{H_1+X}Y-\frac{p_2X}{H_2+X}Z, \tag{1.1}$$

$$\frac{dY}{d\tau} = \frac{b_1p_1X}{H_1+X}Y-d_1Y-\frac{p_3Y}{H_3+Y}W, \tag{1.2}$$

$$\frac{dZ}{d\tau} = \frac{b_2p_2X}{H_2+X}Z-d_2Z, \tag{1.3}$$

$$\frac{dW}{d\tau} = \frac{b_3p_3Y}{H_3+Y}W-d_3W. \tag{1.4}$$

Date:
2000 *Mathematics Subject Classification.* 92D25; 92D40; 37M05.
Key words and phrases. food web; bifurcation; numerical computation.
This research was supported by the Ministry of Science and Technology under the grant MOST103-2115-M-035-005.

The meanings of the parameters are given in the above quoted papers. Using the scaling transformations together with the nondimensional parameters suggested in [5, 6], the nondimensional form of Eqs. (1.1)-(1.4) becomes

$$\zeta\frac{dx}{dt} = x\left(1-x-\frac{y}{\beta_1+x}-\frac{z}{\beta_2+x}\right), \tag{1.5}$$

$$\frac{dy}{dt} = y\left(\frac{x}{\beta_1+x}-\delta_1-\frac{w}{\beta_3+y}\right), \tag{1.6}$$

$$\frac{dz}{dt} = \epsilon_1 z\left(\frac{x}{\beta_2+x}-\delta_2\right), \tag{1.7}$$

$$\frac{dw}{dt} = \epsilon_2 w\left(\frac{y}{\beta_3+y}-\delta_3\right). \tag{1.8}$$

This mathematical model has been studied by varies researchers and proven to have rich dynamics. Without the top-predator w, y and z cannot coexist at a stable equilibrium state due to the competitive exclusion principle. When z goes to extinction, the system becomes a food chain system, and its chaotic dynamics have been studied by Deng and Hines [1, 2, 3, 4]. Bockelman et al. [5] have proven that when w is efficient, coexistence of all species is possible and the noncompetitive z can drive the dynamics from periodic orbits to chaos. Bockelman and Deng [6] have shown that population chaos does not require the existence of oscillators in any subsystem of the web, and chaos occurs via a period-doubling cascade from a Hopf bifurcation point. Wei [7] studied the existence and stability of equilibria using mathematical analysis and computed two-parameter bifurcation diagrams using an adaptive grid method. Interesting dynamics and different cascades leading to chaos were observed from numerical simulations. Wei and Li [8] analyzed a Hopf bifurcation from the equilibrium with $z = 0$ and $w = 0$.

The identification of steady states and their bifurcations is important as a standard process to study a dynamical system. The steady states in a dynamical system often provide insight into the mechanism of biological processes leading to predictions of the biological behavior. Bifurcation analysis is the study of the changes in qualitative or topological structure as parameter values vary, and dynamical systems often exhibit complex dynamics around high codimensional bifurcation points. However, since realistic models are nonlinear and complicated, analytical results are often restricted to particular models with special properties. Numerical analysis is, thus, important for studying the bifurcations of these systems. An adaptive grid technique for bifurcations of equilibria in continuous time dynamical systems has been developed in our previous studies [7, 9]. It does not require the computation of higher derivatives and can be easily applied to the computation of three-parameter bifurcations of equilibria [10].

This paper is a continuation of the work by Wei [7] and focuses on three-parameter bifurcations, as well as codimension-two and -three bifurcations. To provide details, the mathematical analysis of a part of codimension-two bifurcations and the codimension-thee bifurcation is carried out in Section 2. Numerical examples and discussion are presented in Section 3. Section 4 provides a brief conclusion.

2. Mathematical analysis

Wei [7] has studied the conditions for the existence of the equilibria and their stability properties. In this paper, we further derive some conditions of codimension-two and -three bifurcations of equilibria in Eqs. (1.5)-(1.8) using β_1, β_2, and β_3 as bifurcation parameters. A rectangular parameter domain $\Omega = (0,1) \times (0,1) \times (0,1)$ is considered, and the other parameters are fixed as in Table 1. Eqs. (1.5)-(1.8) have eight possible equilibria labeled by P_i, $i = 1, \ldots, 5, 61, 62, 7$, as shown in Table 2 [7]. The notations $(x,y,z,w)_{P_i}$, E_i, and $A(P_i)$ are used for the coordinates, region of existence, and Jacobian matrix of the steady state P_i, respectively, throughout this paper. Also, R_i denotes the region where P_i is stable.

Table 1. Parameter values in Eqs. (1.5)-(1.8)

ζ	ϵ_1	ϵ_2	δ_1	δ_2	δ_3
0.1	0.5	0.1	0.5	0.52	0.54

Table 2. possible equilibria in Eqs. (1.5)-(1.8), $t \in (0,1)$

	P_1	P_2	P_3	P_4	P_5
x	0	1	$\frac{\delta_1\beta_1}{1-\delta_1}$	$\frac{\delta_2\beta_2}{1-\delta_2}$	$\frac{\delta_2\beta_2}{1-\delta_2}$
y	0	0	$(1-x)(\beta_1+x)$	0	$t(1-x)(\beta_1+x)$
z	0	0	0	$(1-x)(\beta_2+x)$	$(1-t)(1-x)(\beta_2+x)$
w	0	0	0	0	0

	P_{61}	P_{62}	P_7
x	$\frac{(1-\beta_1)+\sqrt{(1-\beta_1)^2-4(y-\beta_1)}}{2}$	$\frac{(1-\beta_1)-\sqrt{(1-\beta_1)^2-4(y-\beta_1)}}{2}$	$\frac{\delta_2\beta_2}{1-\delta_2}$
y	$\frac{\delta_3\beta_3}{1-\delta_3}$	$\frac{\delta_3\beta_3}{1-\delta_3}$	$\frac{\delta_3\beta_3}{1-\delta_3}$
z	0	0	$\frac{\beta_2}{1-\delta_2}(1-x-\frac{y}{\beta_1+x})$
w	$(\frac{x}{\beta_1+x}-\delta_1)\frac{\beta_3}{1-\delta_3}$	$(\frac{x}{\beta_1+x}-\delta_1)\frac{\beta_3}{1-\delta_3}$	$\frac{\beta_3}{1-\delta_3}(\frac{x}{\beta_1+x}-\delta_1)$

Theorem 2.1. *The system, Eqs. (1.5)-(1.8), undergoes a double-zero bifurcation, where $A(P_3)$ has two zero eigenvalues, if $\beta_1 = \frac{1-\delta_1}{\delta_1}$ and $\beta_2 = \frac{1-\delta_2}{\delta_2}$ or if $\beta_1 > \frac{1-\delta_1}{1+\delta_1}$, $\beta_2 = \frac{\delta_1(1-\delta_2)}{\delta_2(1-\delta_1)}\beta_1$, and $\beta_3 = \frac{1-\delta_3}{\delta_3(1-\delta_1)}\beta_1(1-\frac{\delta_1}{1-\delta_1}\beta_1)$.*

Proof. We let λ_i, $i = 1, \ldots, 4$, be the eigenvalues of $A(P_3)$. From the work by Wei [7], $(x,y,z,w)_{P_3} = (\frac{\delta_1\beta_1}{1-\delta_1}, (1-x)(\beta_1+x), 0, 0)$, $\lambda_1 + \lambda_2 = \frac{\delta_1}{\zeta}(1 - \frac{\beta_1(1+\delta_1)}{1-\delta_1})$, $\lambda_1\lambda_2 = \frac{\delta_1}{\zeta}(1-\delta_1-\delta_1\beta_1)$, $\lambda_3 = \epsilon_1(\frac{x}{\beta_2+x}-\delta_2)$, and $\lambda_4 = \epsilon_2(\frac{y}{\beta_3+y}-\delta_3)$. Note that if $\lambda_1 = 0$, then $\beta_1 = \frac{1-\delta_1}{\delta_1}$, $x = 1$, and $y = 0$. P_3 coincides with P_2. Also, $\lambda_2 = -1/\zeta < 0$, and $\lambda_4 = -\epsilon_2\delta_3 < 0$. Thus, the system undergoes a double-zero bifurcation if $\lambda_3 = 0$ implying $\beta_2 = \frac{1-\delta_2}{\delta_2}$. The system undergoes the other double-zero bifurcation if $\lambda_1 + \lambda_2 < 0$, $\lambda_1\lambda_2 > 0$, $\lambda_3 = 0$, and $\lambda_4 = 0$. This gives the conditions $\beta_1 > \frac{1-\delta_1}{1+\delta_1}$, $\beta_2 = \frac{\delta_1(1-\delta_2)}{\delta_2(1-\delta_1)}\beta_1$, and $\beta_3 = \frac{1-\delta_3}{\delta_3(1-\delta_1)}\beta_1(1-\frac{\delta_1}{1-\delta_1}\beta_1)$. □

Theorem 2.2. *The system undergoes a fold Hopf bifurcation, where $A(P_3)$ has a zero eigenvalue and a pair of pure imaginary eigenvalues, if $\beta_1 = \frac{1-\delta_1}{1+\delta_1}$ and* *either* $\beta_2 = \frac{\delta_1(1-\delta_2)}{\delta_2(1-\delta_1)}\beta_1$ *and* $\beta_3 > \frac{1-\delta_3}{\delta_3(1-\delta_1)}\beta_1(1-\frac{\delta_1}{1-\delta_1}\beta_1)$ *or* $\beta_2 > \frac{\delta_1(1-\delta_2)}{\delta_2(1-\delta_1)}\beta_1$ *and* $\beta_3 = \frac{1-\delta_3}{\delta_3(1-\delta_1)}\beta_1(1-\frac{\delta_1}{1-\delta_1}\beta_1)$.

Proof. Given λ_i, $i = 1, \ldots, 4$, in the proof of Theorem 2.1, the system undergoes a fold Hopf bifurcation if $\lambda_1 + \lambda_2 = 0$, $\lambda_1\lambda_2 > 0$, and either $\lambda_3 = 0$ and $\lambda_4 < 0$ or $\lambda_3 < 0$ and $\lambda_4 = 0$. With the domain Ω and the parameter values shown in Table 1, this gives the conditions $\beta_1 = \frac{1-\delta_1}{1+\delta_1}$ and either $\beta_2 = \frac{\delta_1(1-\delta_2)}{\delta_2(1-\delta_1)}\beta_1$ and $\beta_3 > \frac{1-\delta_3}{\delta_3(1-\delta_1)}\beta_1(1-\frac{\delta_1}{1-\delta_1}\beta_1)$ or $\beta_2 > \frac{\delta_1(1-\delta_2)}{\delta_2(1-\delta_1)}\beta_1$ and $\beta_3 = \frac{1-\delta_3}{\delta_3(1-\delta_1)}\beta_1(1-\frac{\delta_1}{1-\delta_1}\beta_1)$. □

The system undergoes a codimension-three bifurcation, where $A(P_3)$ has double-zero and a pair of pure imaginary eigenvalues, if $\lambda_1 + \lambda_2 = 0$, $\lambda_1\lambda_2 > 0$, $\lambda_3 = 0$, and $\lambda_4 = 0$. This gives the conditions of the codimension-three bifurcation in the next theorem.

Theorem 2.3. *The system undergoes a fold Hopf bifurcation, where $A(P_4)$ has a zero eigenvalue and a pair of pure imaginary eigenvalues, if $\beta_1 = \frac{\delta_2(1-\delta_1)}{\delta_1(1+\delta_2)}$ and $\beta_2 = \frac{1-\delta_2}{1+\delta_2}$.*

Proof. We let λ_i, $i = 1, \ldots, 4$, be the eigenvalues of $A(P_4)$. From the work by Wei [7], $(x, y, z, w)_{P_4} = (\frac{\delta_2\beta_2}{1-\delta_2}, 0, (1-x)(\beta_2 + x), 0)$, $\lambda_1 + \lambda_2 = \frac{\delta_2}{\zeta}(1 - \frac{\beta_2(1+\delta_2)}{1-\delta_2})$, $\lambda_1\lambda_2 = \frac{\epsilon_1\delta_2}{\zeta}(1-\delta_2-\delta_2\beta_2)$, $\lambda_3 = \frac{x}{\beta_1+x} - \delta_1$, and $\lambda_4 = -\epsilon_2\delta_3$. The system undergoes a fold Hopf bifurcation if $\lambda_1 + \lambda_2 = 0$, $\lambda_1\lambda_2 > 0$, and $\lambda_3 = 0$. This gives the conditions $\beta_1 = \frac{\delta_2(1-\delta_1)}{\delta_1(1+\delta_2)}$ and $\beta_2 = \frac{1-\delta_2}{1+\delta_2}$. □

The bifurcations related to P_5 are not discussed in this paper because P_5 is not an isolated equilibrium, as shown in Table 2, and is always degenerate. Other codimension-two bifurcations determined by the eigenvalues of $A(P_6)$ and $A(P_7)$ will be carried out using numerical computation.

3. Numerical Simulations and Discussion

In this section, bifurcation diagrams are computed using an adaptive grid method by Wei [7, 9], and this adaptive grid method is extended to a three-parameter space and codimension-two bifurcations. Figs. 1(a)-(c) show the region where P_i, $i =$ 4, 61, 62, or 7, exists. Note that P_1, P_2, and P_3, exist in Ω [7]. The surfaces are plotted in Fig. 1(d) to show the coexistence of equilibria.

Next, we compute the stability of the equilibria and codimension-two and -three bifurcations, which are determined by the eigenvalues of the equilibria. The codimension-two bifurcations of P_3 and P_4 are confirmed with the mathematical analysis given in Sec. 2. Fig. 2(a) shows that P_3 is stable in the region R_3. The system undergoes a double-zero bifurcation on the curve $B_{31} = \{(\beta_1, \beta_2, \beta_3) \in \Omega | \beta_1 > 1/3; \beta_2 = 12\beta_1/13; \beta_3 = 46\beta_1(1-\beta_1)/27\}$ or $B_{32} = \{(\beta_1, \beta_2, \beta_3) \in \Omega | \beta_1 = 1; \beta_2 = 12/13\}$ and a fold Hopf bifurcation on the curve $G_{31} = \{(\beta_1, \beta_2, \beta_3) \in \Omega | \beta_1 = 1/3; \beta_2 = 4/13; \beta_3 > 92/243\}$ or $G_{32} = \{(\beta_1, \beta_2, \beta_3) \in \Omega | \beta_1 = 1/3; \beta_2 > 4/13; \beta_3 = 92/243\}$. The point $(\beta_1, \beta_2, \beta_3) = (1/3, 4/13, 92/243)$, where B_{31}, G_{31}, and G_{32} intersect, is a codimension-three point. Fig. 2(b) shows that P_4 is stable in the region R_4. The system undergoes a fold Hopf bifurcation on the curve $G_4 = \{(\beta_1, \beta_2, \beta_3) \in \Omega | \beta_1 = 13/38; \beta_2 = 6/19\}$.

Fig. 3(a) shows the region where P_{61} is stable. Note that B_{31} and G_{32} are the same codimension-two bifurcation curves as shown in Fig. 2(a). In addition,

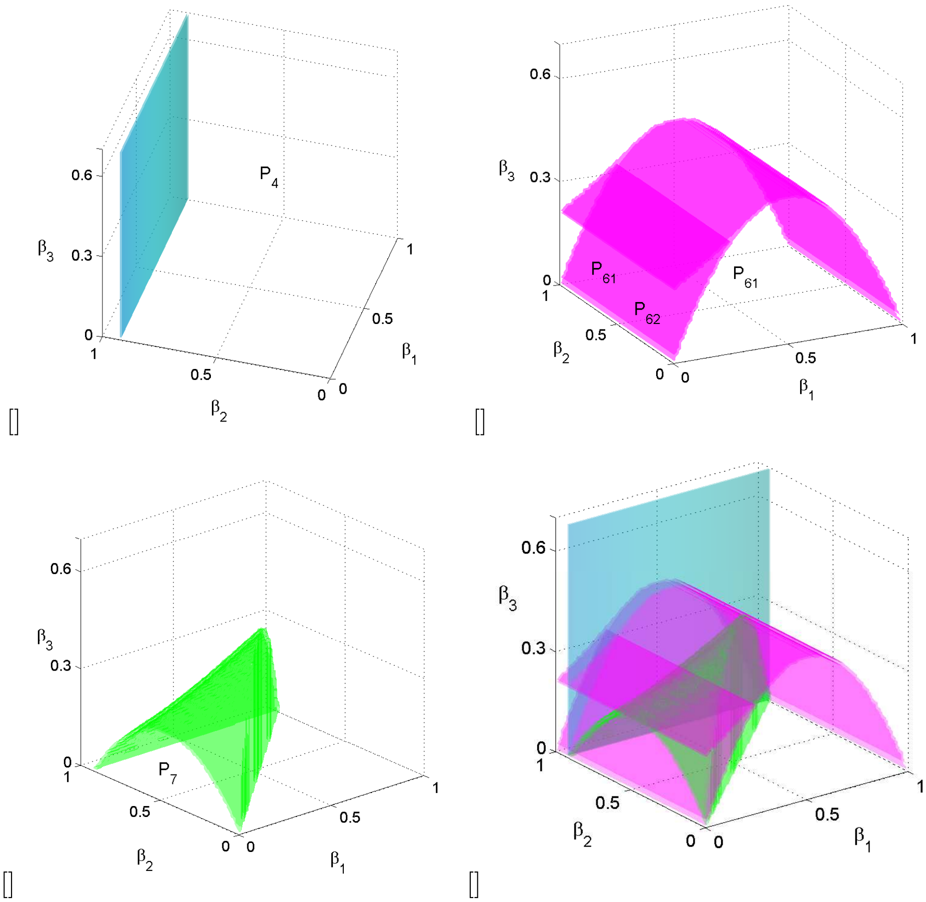

FIGURE 1. The regions where (a) P_4, (b) P_{61} and P_{62}, or (c) P_7 exist. (d) The surfaces shown in (a), (b), and (c) are plotted to show their intersections where coexistence of equilibria occurs.

the system undergoes a fold Hopf bifurcation on the curve G_{61} or G_{62}. Fig. 3(b) shows that P_7 is stable in the region enclosed by the surfaces, and the bifurcation curves B_3 and G_i, $i = 61, 62$, are the same as shown in Fig. 2(a) and Fig. 3(a), respectively. A close look at a part of the region is also shown in this figure. In Fig. 4 we plot all the bifurcation surfaces and curves shown in Figs. 2 and 3.

Finally, a cross section of Fig. 4 (a) at $\beta_2 = 0.57$ is plotted in Fig 5, which is a two-dimensional bifurcation diagram in β_1 and β_3. Note that there are stable limit cycles or chaotic attractors in the regions where none of the equilibria is stable. Fig 5 shows that how the dynamics of the system may be changed with the introduction of the top predator w. Consider the situation that z goes extinct in the absence of w. This occurs in the region for $\beta_1 < 0.6175$ in Fig 5. When β_3 is large, w is not efficient. Neither z nor w can survive. As w becomes more efficient so that β_3 becomes smaller, P_{61} is stable. As β_3 continue to decrease, all species coexist as

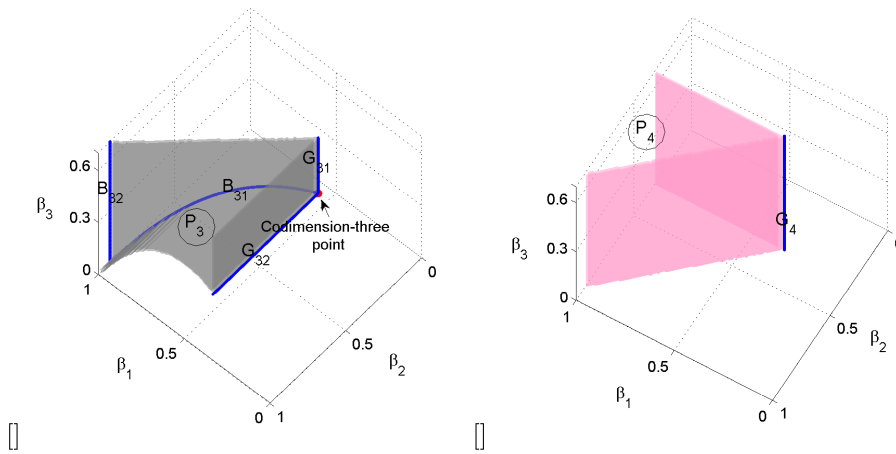

FIGURE 2. The codimension-two and -three bifurcations and the regions where (a) P_3 or (b) P_4 is stable.

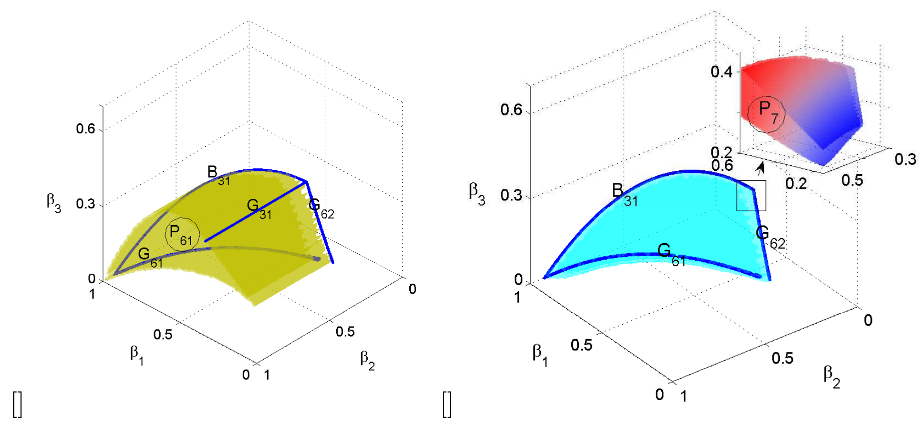

FIGURE 3. The codimension-two and -three bifurcations and the regions where (a) P_{61} or (b) P_7 is stable.

a stable equilibrium. Introducing an efficient top predator increases the possibility of the survival of the inferior competitor that would otherwise go to extinction.

4. CONCLUSION

In this paper, we study the codimension-two and -three bifurcations that are determined by the eigenvalues of equilibria using a food web of four species. An adaptive grid method is employed and modified to compute three-parameter bifurcation diagrams in which codimension-one, -two, and -three bifurcations are located. Conditions of a part of codimension-two bifurcations, as well as the codimension-three bifurcation, are derived using mathematical analysis. These conditions are confirmed with the numerical simulation.

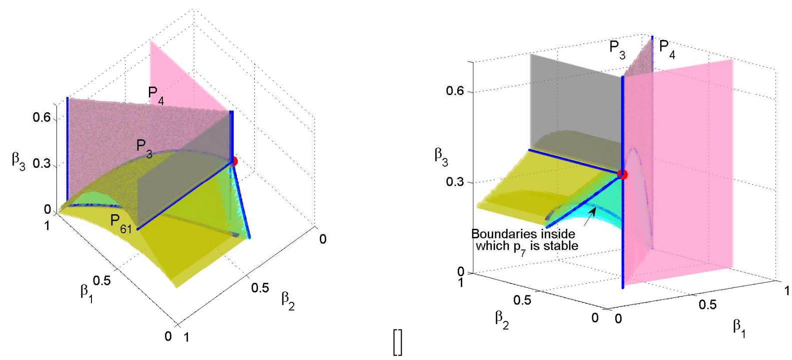

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FIGURE 4. (a) The surfaces shown in Figs. 2 and 3 are plotted to show the relative locations of these bifurcations. (b) Fig 4(a) is rotated to show the location of the region where P_7 is stable.

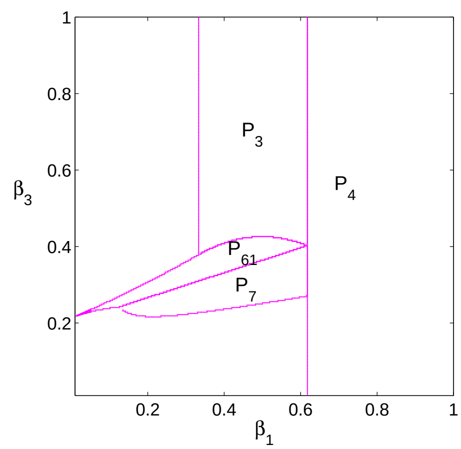

FIGURE 5. A cross section of Fig. 4(a) along the plane $\beta_2 = 0.57$.

Acknowledgment

The author would like to thank Ms. Lisa H. Lin for her help in editing this manuscript.

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Department of Applied Mathematics, Feng Chia University, Seatwen, TaiChung 40724, Taiwan

E-mail address: hsiucwei@fcu.edu.tw