$$y = \frac{a}{b} \tag{12}$$

as seen in Figure 2.

Since

$$\frac{\partial f}{\partial x} = \frac{1}{k}\left[(a - by) - x\right] - \frac{1}{k} \tag{13}$$

it is clear that $\frac{\partial f}{\partial x} < 0$ on the surface given by the equation [11], and thus the nontrivial fast manifold is always stable.

The Intermediate Manifold

This manifold is given by the equation $g = 0$ which defines a surface

$$z = \rho(x, y) \tag{14}$$

It intersects the nontrivial fast manifold along the curve

$$z = \rho(a - by, y) = \frac{\left(d_0 + a\alpha\right)y - \alpha b y^2}{\left(\beta + \pi a\gamma\right) - \pi b\gamma y} \tag{15}$$

We observe that this curve intersects the (x,y)-plane $(z = 0)$ at the points where

$$y = 0$$

and

$$y = \frac{a}{b} + \frac{d_0}{b\alpha} \tag{16}$$

Thus, the curve $f = g = 0$ reaches the (y,z)-plane in the first octant if

$$d_0 > 0 \tag{17}$$

Now, differentiating (15) with respect to y, we find that the numerator of $\frac{dz}{dy}$ along the curve $f = g = 0$ is

$$\mathrm{Num}\left(\frac{dz}{dy}\right)_{f=g=0} = (d_0 + a\alpha)(\beta + \pi a\alpha) - 2b\alpha(\beta + \pi a\gamma)y + \pi b^2\alpha\gamma y^2 \tag{18}$$

Therefore the curve $f = g = 0$ has a stationary point when the left hand side of (18) vanishes. However, we find that the two roots of (18) are

$$y_{1,2} = \frac{2b\alpha(\beta + \pi a\gamma) \pm \Delta}{2\pi b^2\alpha\gamma} = \frac{a}{b} + 2b\alpha\beta \pm \Delta \tag{19}$$

where $$\Delta = 2b\left[(\beta + \pi a\gamma)\left(\alpha^2\beta - \pi\alpha\gamma d_0\right)\right]^{\frac{1}{2}} \tag{20}$$

Thus, for $y_{1,2}$ to be real, we require that

$$\beta > \frac{\pi\gamma\delta_0}{\alpha} \tag{21}$$

Moreover, for at least one root to be less than $\frac{a}{b}$, we need

$$2b\alpha\beta - 2b\left[(\beta + \pi a\gamma)\left(\alpha^2\beta - \pi\alpha\gamma d_0\right)\right]^{\frac{1}{2}} < 0 \tag{22}$$

Squaring and rearranging (22) lead to the requirement that

$$\beta > \frac{\pi a\gamma d_0}{a\alpha - d_0} \tag{23}$$

provided

$$a\alpha - d_0 > 0 \tag{24}$$

At this point, we note that since

$$\frac{\pi a\gamma d_0}{a\alpha - d_0} > \frac{\pi\gamma d_0}{\alpha} \tag{25}$$

the conditions (21) and (23) are quaranteed by the requirement that (23) and (24) hold.

The Slow Manifold

This is the surface $h = 0$ which defines a surface

$$z = \varphi(x, y) \tag{26}$$

that intersects the fast manifold $f = 0$ along the curve given by

$$z = \varphi(a - by, y) \;\; = \frac{a\alpha y - b\alpha y^2}{(d_1 + a\gamma) - b\gamma y} \tag{27}$$

for which $z = 0$ when $y = 0$ and $y = \frac{a}{b}$ (see Figure 2).

Thus, we can identify essentially 5 cases of different dynamical behavior as follows.

<u>Case 1</u>

This case is identified by the inequalities (23) and (24). The shape of the fast manifold is therefore as shown in Figure 2(a) and the curve $f = g = 0$ has a stationary point P above the (y, z)-plane and intersects the (y, z)-plane at the point H in the first octant.

Now, to also guarantee that the point S where $f = g = h = 0$ is below the point P we need that at $y = y_2$ we have

$$\frac{a\alpha y_2 - b\alpha y_2^2}{(d_1 + a\gamma) - b\gamma y_2} > \frac{(d_0 + a\alpha)y_2 - \alpha b y_2^2}{(d_1 + \pi a\gamma) - \pi b\gamma y_2} \tag{28}$$

using (15) and (27).

Inequality (28) means that the part of the curve $f = g = 0$ from C to P lies "above" the surface $h = 0$ while the line DG lies "below" the surface $h = 0$. Looking at the sign of h, we see that $h > 0$ along CP and $h < 0$ along DG which determines the directions of the transients along these curves as shown in Figure 2(a). Moreover, for the curve $f = g = 0$ and $f = h = 0$ to be located with respect to each other as shown in Figure 2(a) we require that at $y = 0$, the slope along the curve $f = g = 0$ should be less than that along the curve $f = h = 0$. That is, we need

$$\left.\frac{dz}{dy}\right|_{f=g=0} < \left.\frac{dz}{dy}\right|_{f=h=0}$$

which leads to the inequality

$$\frac{d_0 + a\alpha}{\beta + \pi a\gamma} < \frac{a\alpha}{d_1 + a\gamma}$$

or

$$\beta > \frac{(d_0 + a\alpha)(d_1 + a\gamma)}{a\alpha} - \pi a\gamma \tag{29}$$

Starting from some initial point, say A (see Figure 2(a)), if A is above the nontrivial fast manifold, $f < 0$ here and a high speed transition will develop in the direction of decreasing x towards the stable fast manifold (point B). As B is approached, the intermediate system has become active and, since $g < 0$ here, a transition of intermediate speed will develop along the fast manifold towards point C on the curve $f = g = 0$. As mentioned above, along this portion of the curve, $h > 0$ and so a slow transition develops in the direction of increasing z until the point P is reached, at which point the stability of the manifold is lost. A transition at a very high speed then takes place which brings us to the point D on the trivial manifold $x = 0$. Since we are now in the region where $h < 0$, transition develops slowly along the line $y = \frac{b}{a}$ until a point E is reached where the stability is again lost. The existence of such a point E in a similar system has been shown in a previous work by Osipov *et al.* [18]. For the point E to be to the right of G as in Figure 2(a), we further require that the second coordinate y_E of this point is positive, namely

$$y_E > 0 \tag{30}$$

However, considering (16), this is easily accomplished if b is made sufficiently small.

A quick jump from E will then take us back to the point F on the curve $f = g = 0$ which completes the closed cycle FPDEF in this case.

Thus, this is the case where the attractor is a limit cycle composed of a concatenation of catastrophic transitions occurring at different speeds, corresponding to the situation where persistence in the toxicant levels and the population density is observed exhibiting sustained oscillations in all three state variables.

Case 2

This case is shown in Figure 2(b), identified by the inequalities (24), (29) and the one opposite to (23), namely

$$\frac{\pi a\gamma d_0}{a\alpha - d_0} > \beta \tag{31}$$

This last inequality means that, in this case, the stationary point of the curve $f = g = 0$ is below the (y, z)-plane and the position of the manifolds are as shown in Figure 2(b).

Starting at an initial point A, transitions will develop as described before until C is reached, from which point a slow transition brings us to a stop at the stable equilibrium point S where $f = g = h = 0$.

This therefore corresponds to the case where population density and both toxicant levels attain stable equilibrium values as time passes.

Case 3

This case is identified by inequalities (23), (24) and the one opposite to inequality (29), namely

$$\beta < \frac{(d_0 + a\alpha)(d_1 + a\gamma)}{a\alpha} - \pi a\gamma \tag{32}$$

Thus , in this case, once we are at the point B on the fast manifold (see the Figure 2(c)), $h < o$ here and a slow transition will develop along the curve $f = g = 0$ in the direction of decreasing z instead. This takes us to a stop on the x-axis ($y = z = 0$)

This is therefore the case where toxicants eventually get depleted and the population re-establishes itself as time passes.

Case 4

This case is identified by the inequalities (23), (24), (29), and the opposite to inequality (28), namely

$$\frac{a\alpha y_2 - b\alpha y_2^2}{(d_1 + a\gamma) - b\gamma y_2} < \frac{(d_0 + a\alpha) - \alpha b y_2^2}{(d_1 + \pi a\gamma) - \pi b\gamma y_2} \tag{33}$$

This last inequality means that the point S is above P on the curve $f = g = 0$ as seen in Figure 2(d).

Again the transitions develop from A to B then to C as before. However, a slow transtion from C will stop at the point S since here $f = g = h = 0$. This is also the case where each state variable attains an equilibrium value as time progresses.

Case 5

This last case is identified by (23), (24), (29), and

$$y_E < 0 \tag{34}$$

However, considering (16), condition (34) can be satisfied if b is made sufficiently large.

The manifolds are then positioned as shown in Figure 2(e). The transitions, once P is reached, will make a quick jump to the point D on the (y, z)-plane. Since the trivial manifold is stable troughout the line DG in this case, the slow transition from D will continue until G is reached where $g < 0$. Transition is then made toward the origin. This then corresponds to the case where the population becomes extinct and the toxicant in the population of course gets depleted as a result, while the toxicant level in the environment reaches a high level then slowly depletes itself as time passes.

By the above analysis, we have proved the following theorem.

Theorem If ε and δ are sufficiently small and inequalities (21) and (24) hold, then the system (4)-(6) has a unique global attractor in the first octant. The attractor will be a stable equilibrium point if (23), (29) and (33) hold or (29), and (31) hold, while it will be a limit cycle if inequalities (23), (28), (29) and (30) hold.

Numerical simulations of the system (4) - (6) when the parametric values are chosen to satisfy the requirements in each of the 5 cases are shown in Figure 3.

CONCLUSION

In this paper, we have analyzed a model for the effects of a toxin introduced into the environment of a single-species system. The population growth is logistic, while the time responses of the different state variables are assumed to increase from bottom to top. We have been able to identify five separate cases in which different dynamic behavior can be observed.

It has been shown that if the rate β at which the toxicant in the population re-enters the environment is higher than the levels given by inequilities (21) and (23) then toxicant will not get depleted to allow the population to recover its former level. If this is further compounded by the condition where the effect of toxicant on the birth-rate is too high ($b >> 1$) then we can expect extinction of the species which is case 5 identified above.

Thus, the model has proved to be quite versatile and fits well with field observations, yielding greater insights into this perplexing problem of interactions among the population and the toxicants in the environment which is of great concern to us all.

ACKNOWLEDGEMENT

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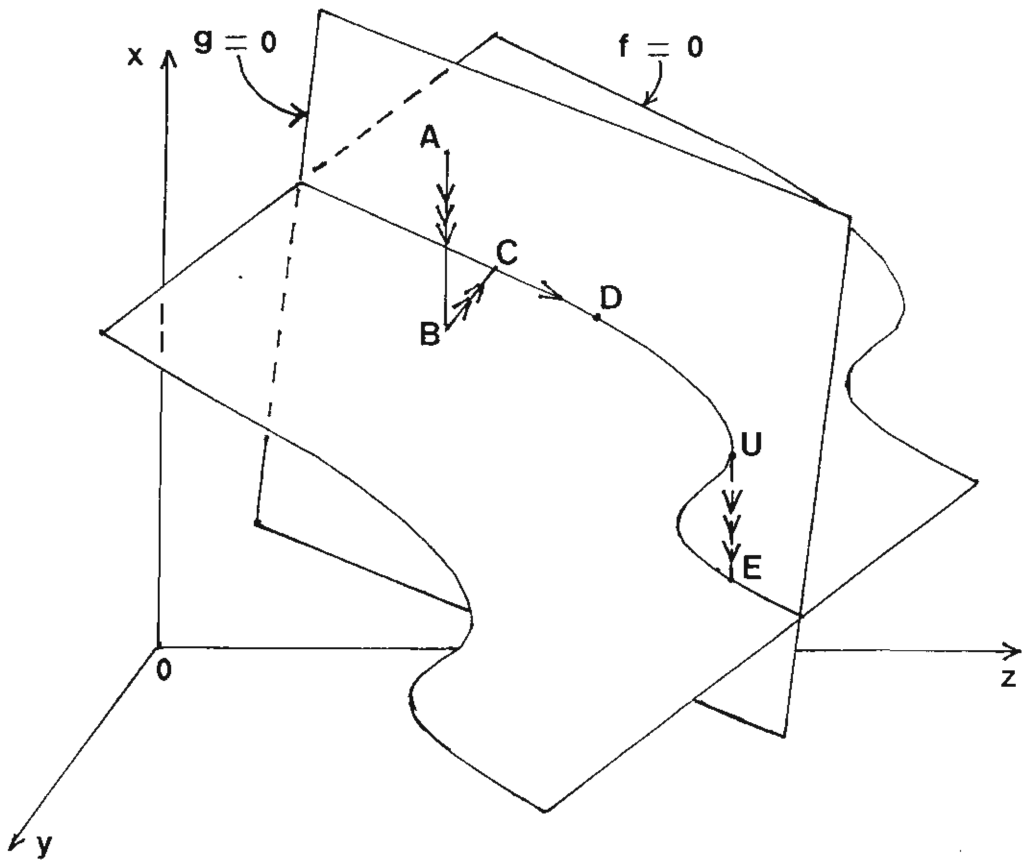
FIGURE CAPTION

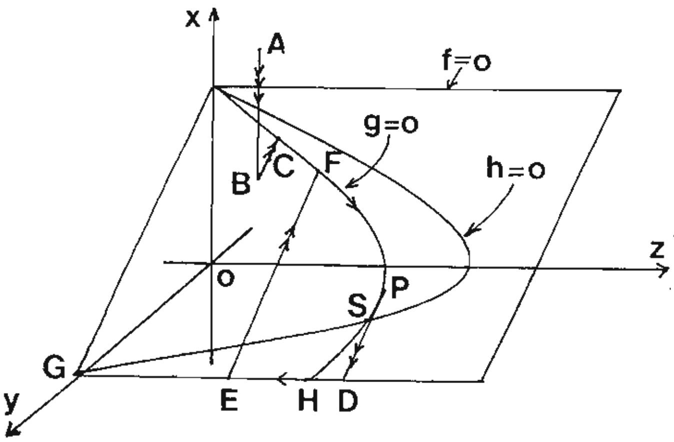
Figure 1: A fast ($f = 0$), intermediate ($g = 0$), and slow ($h = 0$) equilibrium manifolds, with the fast (triple arrow), intermediate (double arrow) and slow (single arrow) transients.

Figure 2: The solution trajectories of the system (4)-(6) in the five cases identified in the text. The attractor is a limit cycle in Case 1, and an equilibrium in Case2, or 4. The population recovers itself in Case3, but becomes extinct in Case 5.

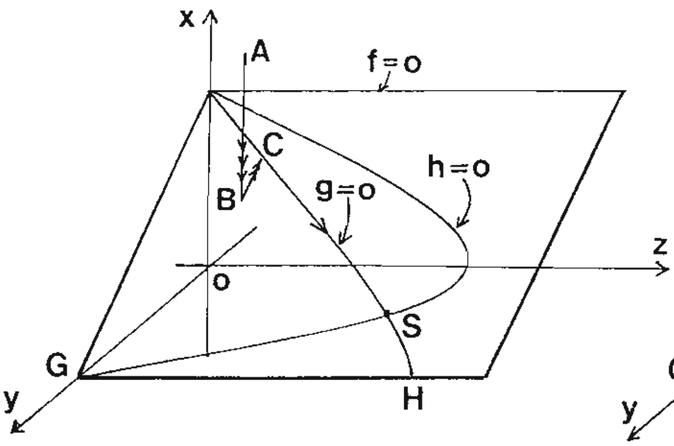
Figure 3: Numerical simulations of the system (4)-(6) for each of the five cases identified in the text. Here, $\varepsilon = \delta = k = 1$; Case1: $a = 0.5$, $b = 0.1$, $\alpha = 0.9$, $\beta = 0.9$, $\gamma = 0.9$, $\pi = 0.9$, $d_0 = 0.3$, $d_1 = 0.01$; Case 2: $a = 0.9$, $b = 0.1$, $\alpha = 0.5$, $\beta = 0.9$, $\gamma = 0.9$, $\pi = 0.9$, $d_0 = 0.4$, $d_1 = 0.01$; Case 3: $a = 0.5$, $b = 0.1$, $\alpha = 0.9$, $\beta = 0.5$, $\gamma = 0.9$, $\pi = 0.1$, $d_0 = 0.3$, $d_1 = 0.01$; Case 4: $a = 0.9$, $b = 0.1$, $\alpha = 0.5$, $\beta = 0.9$, $\gamma = 0.9$, $\pi = 0.9$, $d_0 = 0.1$, $d_1 = 0.5$; Case 5: $a = 0.5$, $b = 0.1$, $\alpha = 0.9$, $\beta = 0.9$, $\gamma = 0.9$, $\pi = 0.9$, $d_0 = 0.001$, $d_1 = 0.01$.



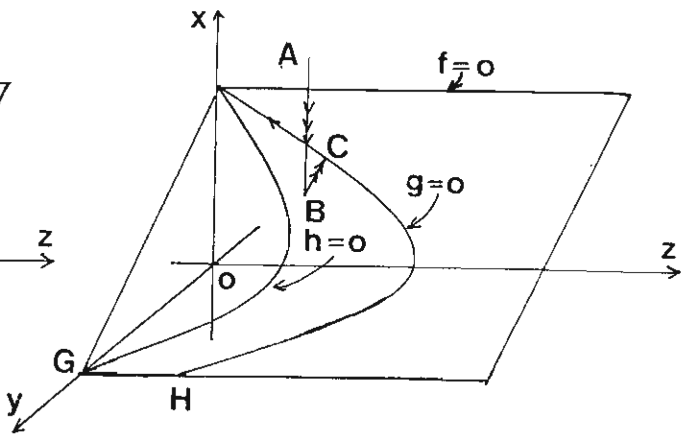
x
g = 0
f = 0
A
C
B
D
U
E
0
z
y



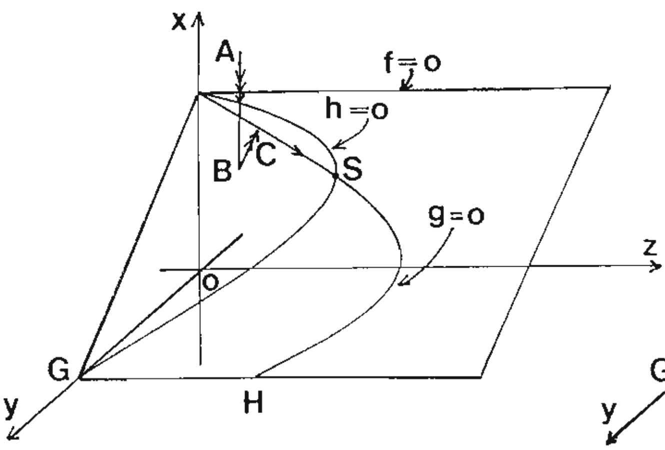
a) Case 1



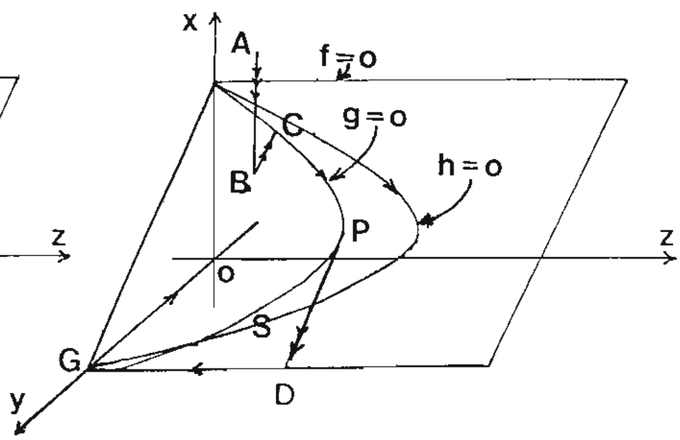
b)Case 2



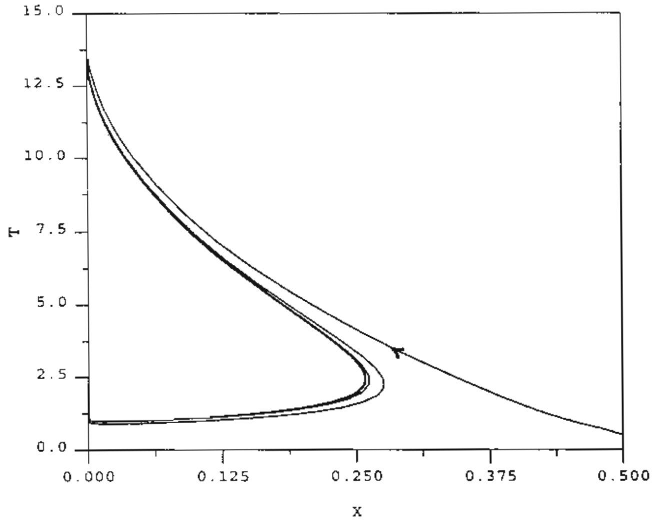
c) Case 3



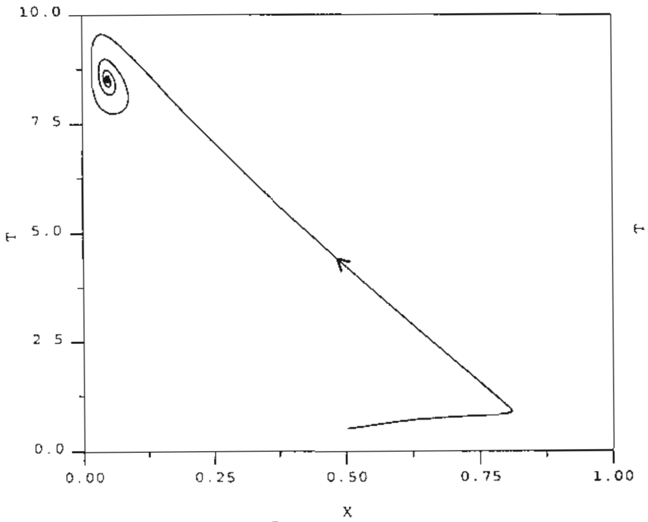
d) Case 4



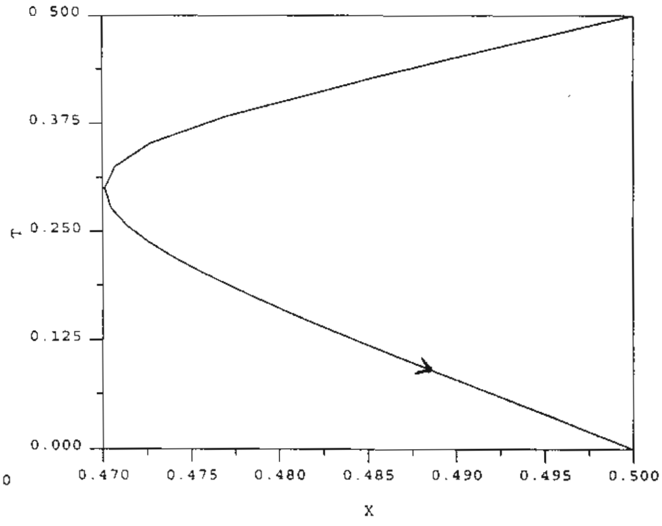
e) Case 5



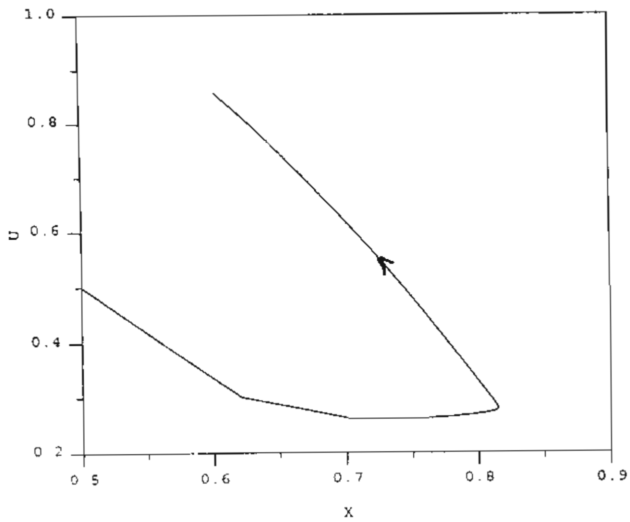
Case 1



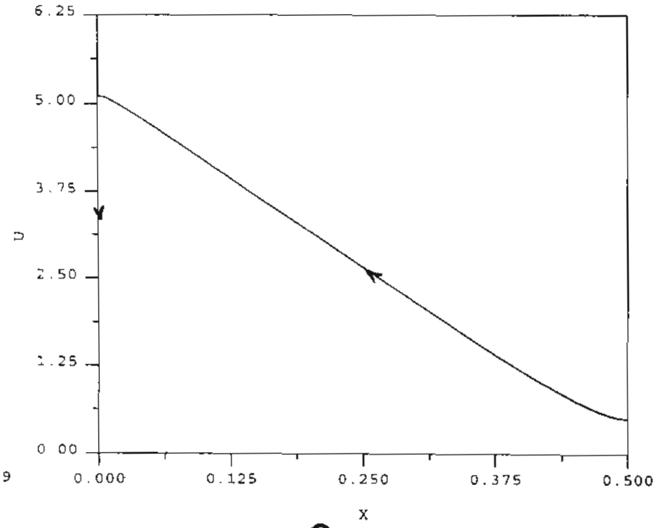
Case 2



Case 3



Case 4



Case 5

4.2 ผู้วิจัยยังได้ทำการวิเคราะห์ model system (62)-(64) โดยใช้ bifurcation analysis เพื่อพิจารณาแบ่งแยก phase space ลักษณะต่าง ๆ ตามจำนวนของ transients และ attractors ได้เป็น phase space 11 แบบที่แตกต่างกัน

ผลงานวิจัยในส่วนนี้ได้นำเขียนขึ้นเป็น paper และได้รับตีพิมพ์แล้วใน *The Mahidol University Journal* ตามเอกสารที่แนบมาด้วยต่อไปนี้

Dynamical Modelling of the Effect of Toxicants on a

Single-Species Ecosystem

DYNAMICAL MODELLING OF THE EFFECT OF TOXICANTS ON A SINGLE-SPECIES ECOSYSTEM

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DYNAMICAL MODELLING OF THE EFFECT OF TOXICANTS ON A SINGLE-SPECIES ECOSYSTEM

ABSTRACT

We consider a mathematical model of the effect of toxicants on single-species in a closed homogeneous environment. The population birth-rate as well as the carrying capacity are assumed to be directly effected by the level of toxicant in the environment as it is absorbed by the population. The toxicant level in the population can be depleted at a constant specific rate, a part of which amount may return to the environment even in the absence of any living organisms. A Hopf bifurcation analysis is carried out yielding boundary conditions which divide the parametric plane into regions of different dynamical behavior. It is found that when the natural birth rate of the population is too low, no non-trivial equilibrium state exists in the system. At a fixed sufficiently high natural birth rate, the system can settle back to its former stable equilibrium state after the initial dumping of toxicant into the environment, provided that the rate at which the toxicant in the population returns to the environment is not too high. Sustained oscillation in the population and toxicant levels is exhibited for suitable ranges of parametric values. However, if the per capita decay rate or birth rate is too low, the system no longer admits a stable non-trivial equilibrium state if the return rate is too high, and population may become extinct.

Keywords: toxicants, modelling, single species, bifurcation.

INTRODUCTION

The question of effects of pollutants and toxicants on ecological communities has become of grave concern to scientists, environmental agencies and authorities on a global scale, especially in the past decade or so. Toxic substances are persistent and bioaccumulate, and therefore contaminate air, water, and most living organisms, including humans. Accidental intoxication by these substances can result in chronic effects and the possible toxicological consequences can no longer be disregarded. In one of their papers, Xober and Papke [1] reports the incidents where concentrations of Polychlorinated Dibenzo-p-dioxins and Dibenzofurans (PCDDs and PCDFs) in human tissues can be detected 36 years after accidental dioxin exposure.

Several efforts have been made to qualitatively describe and study the effects of toxicants and pollutants on various ecosystems. In a series of papers by Hallam and his coworkers [2-5], analytical study was caried out utilizing various mathematical models. Shukla *et al.* [6] later studied a mathematical model for the degradation and subsequent regeneration of forestry resource. More recently, in papers by Carrier *et al.* [7-8] , attempts were made to model the toxicokinetics of PCDDs and PCDFs in mammalians, including humans.

Realistically, a great number of sociological and physiological factors play a part in the dynamics of toxicological pathways in nature. The resulting mathematical model can be quite complexed, handled mainly by powerful computers, and requires a great number of field data for its validation.

A relatively less complicated model involving only a few mathematical equations is often preferred for its capability to give a deep understanding and a great deal to new valuable insights to the system under study, while requiring fewer data for its verification. It can moreover give policy makers the much needed preliminary information to justify their decision or choice of actions concerning important environmental issues.

In [9], Freedman and Shukla proposed a model for the effect of toxicant in single species systems and one for predator-prey polluted systems. The interactions of the population level (X) and toxicants in the population (U) and in the environment (T) are modelled by means of ordinary differential equations in terms of their concentrations with respect to mass or volume of the total environment in which the population lives.

In their model for a single-species system, the amount of toxicant in the population is depleted due to their death, some of which re-entering the environment in proportion to the population biomass. Such a model was found to exhibit no oscillatory behavior in the case that there is no more dumping of toxicants after the initial instantaneous introduction. It was shown that provided that the pollutant concentration was not sufficient to kill all the population, eventually the toxicant would be removed and the population would recover to its former level. However, cases have often been found in nature in which this is not so, and persistence of toxicant levels in the population and the environment have often been observed such as in the earlier mentioned paper by Xober and Papke [1].

In this paper, we therefore consider single-species in a closed homogeneous environment, in which the carrying capacity and the population birth-rate are both affected by the exogeneous introduction of toxicant. By modifying the model proposed by Freedman and Shukla [9], we allow the toxicant in the population to re-enter the environment, a part of which amount varies directly as the toxicant level in the population alone. This will account for the portion of toxicant in the population carcasses which may keep re-entering the closed environment even in the dwindling presence ($x \cong 0$) of the living organism.

We are interested in determining the different dynamics that may result from the effects of toxicants on such a closed ecosystem. Application of the Hopf bifurcation analysis allows us to derive boundary conditions which delineate the parametric plane into regions of different dynamic behavior. It is shown that, after an initial dumping of toxicant into the environment, if the toxicant level in the population and the environment keep decaying at a constant per capita degradation rate, the system can settle back to its former stable equilibrium state provided that the rate at which toxicant in the population re-enters the environment is not too high. However, if the natural birth rate is too low, the non-trivial equilibrium state no longer exists. Moreover, even for high natural birth rate, the equilibrium state can become unstable, and sustained oscillation in the population and toxicant levels is observed if the return rate is high enough.

THE SYSTEM MODEL

Following Freedman and Shukla [9], we let

$$X(t) = \frac{\text{concentration of the population biomass}}{\text{mass (or volume) of the total environment where the population lives}}$$

$$T(t) = \frac{\text{concentration of the toxicant in the environment}}{\text{mass (or volume) of the total environment where the population lives}}$$

$$U(t) = \frac{\text{concentration of the toxicant in the total population}}{\text{mass (or volume) of the total environment where the population lives}}$$

It shall be assumed that the population growth is logistic, while the absorbtion of the toxicant in the environment by the population causes the birth-rate (R) of X to diminish. We therefore assume that R depends explicitly on T with the following properties:

$$R(0) = r_0 > 0 \tag{1}$$

$$R(T) < 0 \quad \text{for } T \geq 0 \tag{2}$$

and $$R(\bar{T}) = 0 \quad \text{for some } \bar{T}. \tag{3}$$

The carrying capacity K(T) of the environment is also effected by the level of toxicant in the environment and has the following general properties

$$K(T) = K_0 > 0 \tag{4}$$

and $$K'(T) < 0 \quad \text{for } T \geq 0. \tag{5}$$

The toxicant levels in the environment, and in the population, have natural depletion (or decaying) rates of δ_0 and δ_1, respectively. The toxicant in the environment is also depleted at a per capita rate α_1 due to its intake by the population. On the other hand, the toxicant in the population is depleted at a per capita rate of γ due to death or removal, a fraction of which amount re-enters the environment. We therefore arrive at the following system of ordinary differential equations.

$$\frac{dX}{dt} = R(T)X - \frac{r_0 X^2}{K(T)} \tag{6}$$

$$\frac{dT}{dt} = -\delta_0 T - \alpha_1 XT + f(X,U) \tag{7}$$

$$\frac{dU}{dt} = -\delta_1 U + \alpha_1 XT - \gamma_1 XU \tag{8}$$

where the last term f(X,U) of equation (7) accounts for the fraction of toxicant in the population which returns to the environment. Since this return rate must increase with the increase in X or U, while in the absence of living organisms ($X = 0$) toxicant can still keep re-entering the environment at a positive rate which necessarily depends on the level of toxicant in the population (U) at that moment in time. The function f(X,U) is thus assumed to have the form

$$f(X,U) \equiv \pi\gamma_1 XU + \beta U \tag{9}$$

where π, γ_1, and β are positive constants.

STEADY STATES AND THEIR STABILITY

For the following analysis, we shall assume that the population natural birth-rate has the form

$$R(T) = r_0 - r_1 T\ , \quad r_0 > 0, r_1 > 0. \tag{10}$$

which satisfies the properties (1)-(3) with $r_0 >$ and $\overline{T} = \frac{r_0}{r_1}$. We will also carry out the analysis for the case where the effect of toxicant on the carrying capacity K is negligible and therefore K = constant.

In order to carry out the stability analysis, we introduce the following change of variables and system parameters : $x = \frac{r_0 X}{K}$, $y = T$, $z = U$, $a = r_0$, $b = r_1$, $d_0 = \delta_0$, $\alpha = \frac{K\alpha_1}{r_0}$, $\gamma = \frac{K\gamma_1}{r_0}$, and $d_1 = \delta$

The model equations (6)-(8) with (9) can then be written as

$$\frac{dx}{dt} = (a - by)x - x^2 \tag{11}$$

$$\frac{dy}{dt} = -d_0 y - \alpha xy + \pi\gamma xz + \beta z \tag{12}$$

$$\frac{dz}{dt} = -d_1 z + \alpha xy - \gamma xz \tag{13}$$

The system of equations (11)-(13) thus admits three steady states, namely

i) the washout steady state: $(x,y,z) = (0,0,0)$

ii) washout of toxicant only : $(x,y,z) = (a,0,0)$

iii) the nonwashout steady state(s), $(\bar{x}, \bar{y}, \bar{z})$ satisfying

$$(a - b\bar{y}) - \bar{x} = 0 \tag{14}$$

$$-d_0\bar{y} - \alpha\bar{x}\bar{y} + \pi\gamma\bar{x}\bar{z} + \beta\bar{z} = 0 \tag{15}$$

$$-d_1\bar{z} + \alpha\bar{x}\bar{y} - \gamma\bar{x}\bar{z} = 0 \tag{16}$$

Solving equations (14)-(16) for $\bar{x}$, we find

$$\bar{x}_{1,2} = \frac{\delta \pm \sqrt{\delta^2 - 4(1-\pi)\alpha\gamma d_0 d_1}}{2(1-\pi)\alpha\gamma} \tag{17}$$

where

$$\delta = \alpha\beta - d_0\gamma - d_1\alpha$$

Then

$$\bar{y} = \frac{a - \bar{x}}{b}$$

and $$\bar{z} = \frac{\alpha\bar{x}\bar{y}}{d_1 + \gamma\bar{x}} = \frac{\alpha\bar{x}(a - \bar{x})}{d_1 + \gamma\bar{x}}$$

We note that if

$$\beta < \frac{d_0\gamma + d_1\alpha}{\alpha} \tag{18}$$

then $\delta < 0$ and both $\bar{x}_1$ and $\bar{x}_2$ are negative and have no physical meaning in our system. Moreover, for values of β such that

$$\delta^2 < 4(1-\pi)\alpha\gamma d_0 d$$

the term under the square root sign in (17) is negative. The system therefore admits only the washout steady states until β crosses the critical value

$$\beta_c \equiv \frac{1}{\alpha}\,[2\sqrt{(1-\pi)\alpha\gamma d_0 d_1} + d_0\gamma + d_1\alpha] \tag{19}$$

at which point the system undergoes a saddle node bifurcation and two more steady states appear which move further apart as β increases. As β increases even further, one of the roots given in (17) becomes negative as shown in Figure 1, and the bigger β gets the roots can become either negative or bigger than a, in which case $\bar{y} = \dfrac{a-\bar{x}}{b} < 0$, leaving us with only the two washout steady states, as shown in the bifurcation diagram presented in Figure 1.

The Jacobian matrix evaluated at the trivial steady state (0,0,0) is

$$J_0 = \begin{bmatrix} a & 0 & 0 \\ 0 & -\delta_0+\beta & 0 \\ 0 & 0 & -\delta_1 \end{bmatrix} \tag{20}$$

one of whose eigenvalues is always positive (namely a), and one is always negative ($-\delta$). This means that the washout steady state (0,0,0) is a saddle point for all positive values of the system parameters and thus the dashed line along the β-axis signifying that the trivial steady state $\bar{x}=0$ is unstable.

The Jacobian matrix of the system (11-(13) evaluated at the steady state (a,0,0) is

$$J_a = \begin{bmatrix} -a & -ab & 0 \\ 0 & -d_0 - \alpha a & \pi\gamma a + \beta \\ 0 & \alpha a & -d_1 - \gamma a \end{bmatrix}$$

and the corresponding eigenvalues are -a and

$$\frac{\Delta \pm \sqrt{\Delta^2 - 4[(d_0 + \alpha a)(d_1 + \gamma a) - \alpha a(\pi\gamma a + \beta)]}}{2} \qquad (21)$$

where

$$\Delta = -d_0 - d_1 - \alpha a - \gamma a.$$

Expanding Δ^2, we find that the term under the square root sign in (21) is always positive. Moreover, the term will be less than Δ^2 if

$$\beta < \frac{(d_0 + \alpha a)(d_1 + \gamma a)}{\alpha a} - \pi\gamma a \equiv \beta' \qquad (22)$$

in which case the steady state (a,0,0) will be a stable node since $\Delta < 0$. On the other hand if

$$\beta > \beta' \qquad (23)$$

then the point will be an unstable saddle point since one of the eigenvalues will be positive.

The Jacobian matrix evaluated at the nontrivial steady state $(\bar{x},\bar{y},\bar{z})$, whenever it exists, is

$$\bar{J} = \begin{bmatrix} -\bar{x} & -b\bar{x} & 0 \\ -\alpha\bar{y}+\pi\gamma\bar{z} & -d_0-\alpha\bar{x} & \pi\gamma\bar{x}+\beta \\ \alpha\bar{y}-\gamma\bar{z} & \alpha\bar{x} & -d_1-\gamma\bar{x} \end{bmatrix} \qquad (24)$$

when $\bar{x}$, $\bar{y}$, and $\bar{z}$ satisfy equations (14) through (16). The corresponding characteristic equation is

$$\lambda^3+a_2\lambda^2+a_1\lambda+a_0 = 0. \qquad (25)$$

where

$$a_0 = b\bar{x}\left[(\pi\gamma\bar{z}-\alpha\bar{y})(d_1+\gamma\bar{x})+(\pi\gamma\bar{x}+\beta)(\alpha\bar{y}-\gamma\bar{z})\right] \qquad (26)$$

$$a_1 = \bar{x}\left[d_0+d_1+(\alpha+\gamma)\bar{x}\right]+b\bar{x}(\pi\gamma\bar{z}-\alpha\bar{y}) \qquad (27)$$

$$a_2 = d_0+d_1+(1+\alpha+\gamma)\bar{x} \qquad (28)$$

If we let

$$q = \frac{1}{3}a_1-\frac{1}{9}a_2^2 \qquad (29)$$

$$r = \frac{1}{6}(a_1a_2-3a_0)-\frac{1}{27}a_2^3 \qquad (30)$$

$$S_1 = [r+(q^3+r^2)^{\frac{1}{2}}]^{\frac{1}{3}} \qquad (31)$$

$$S_2 = [r-(q^3+r^2)^{\frac{1}{2}}]^{\frac{1}{3}} \qquad (32)$$

In region II, however, $a_0 > 0$ while $a_1a_2 > a_0$ and the real parts of all 3 eigenvalues are negative. The non-trivial steady state is therefore a stable spiral node in this case. As time passes, all trajectories starting from its neighborhood will spiral toward the equilibrium point where $\bar{x} = \bar{x}_2$.

In region III, $a_0 > 0$ and $a_1a_2 < a_0$ and limit cycle behavior can be observed resulting from a Hopf bifurcation from the steady state solution which has now become unstable. It is found numerically that the bifurcated limit cycle is stable throughout this region.

Schematic diagram of different dynamic behavior and transients which may be observed in each of the 10 ranges of parametric value β; namely, A through J, are shown in Figure 1. Here, solid lines indicate stability, dashed ones indicate unstability, while closed dots represent stable limit cycles resulting from supercritical bifurcation and increasing in amplitude as β increases. The numbers of possible transients or attractors in each of the 10 ranges, A through J, are given in Table 1.

In fact, substituting (26)-(28) into (40) and (42), we find that Hopf bifurcation occurs for values of β for which $a_1a_2 < a_0$ or equivalently,

$$\beta > \beta_1^* \equiv \frac{a_2 x_2(\theta_1+\theta_2)+(a_2-\theta_1)(\pi\gamma\bar{z}_2-\alpha\bar{y}_2)b\bar{x}_2}{b\bar{x}_2(\alpha\bar{y}_2-\gamma\bar{z}_2)} - \pi\gamma\bar{x}_2 \qquad (43)$$

as well as $a_0 > 0$ which is equivalent to

$$\beta > \beta_2^* \equiv \frac{(\pi\gamma\bar{z}_2-\alpha\bar{y}_2)\theta_1}{\gamma\bar{z}_2-\alpha\bar{y}_2} - \pi\gamma\bar{x}_2 \qquad (44)$$

where

$$\bar{y}_2 = \frac{a-\bar{x}_2}{b}$$

$$\bar{z}_2 = \frac{\alpha\bar{x}_2\bar{y}_2}{d_1+\gamma\bar{x}_2}$$

with

$$\theta_1 = d_0 + \alpha\bar{x}_2$$

$$\theta_2 = d_1 + \gamma\bar{x}_2$$

Thus, Hopf bifurcation occurs for values of β such that

$$\beta > \max(\beta_1^*, \beta_2^*) \tag{45}$$

In Figure 1, four different possibilities in region III are schemetically shown according to the value of β' relative to the values β_c, β_1^* and β_2^*.

Finally, numerical simulations of the model system (11)-(13) in the different cases discussed above are shown in Figure 3, in which parametric values for Figures 3(a), 3(b), and 3(c) are chosen to be in region I, II, and III of Figure 2, respectively. The corresponding time series of the various cases are shown in Figure 4, where sustained oscillation is observed when the paremetric values fall inside the region III where periodic solution has been predicted. In region II, on the other hand, the trajectory is seen to first approach the origin, which is a saddle point, then gets repulsed as the population recovers itself and returns to its equilibrium value at the stable steady state (a, 0, 0). However, if in this region we have a very low degradation rate and birth rate and very high return rate, the population level x is capable of dropping all the way to zero. The toxicant level reaches a high level so fast that the population does not have time to recover itself, in which case the population can become extinct.

CONCLUSION

We have considered a mathematical model of the effect of toxicants on a single species system in a closed homogeneous environment. Application of the Hopf bifurcation analysis led us to the conclusion that if the return rate β, namely the rate at which the toxicant in the population re-enters thee environment is sufficiently low, a stable non-trivial equilibruim state exists in which case the population persists while the toxicant level may degenerate to zero or tend toward an acceptable level. However, for a fixed value of the self degradation rate d_0 and birth rate r_0, if β increases beyond the critical values β_1^* and β_2^* given in the paper, the system becomes unstable and the toxicant level can rise to an undesirably high level. Through our analysis, we found that the system can exhibit up to 10 different types of phase space, and a possibility of up to 5 transients or attractors.

This study of the various dynamic behavior which is possible in such an important process should serve as a useful tool for trying to understand and efficiently control such interesting but complexed ecosystems.

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	A	B	C	D	E	F	G	H	I	J
stable node	1	-	2	1	1	1	3	2	2	2
unstable node	-	-	-	1	1	-	-	1	1	-
saddle point	1	2	2	2	2	2	1	1	1	1
limit cycle	-	-	-	1	-	-	-	1	-	-
Total	2	2	4	5	4	3	4	5	4	3

Table 1

FIGURE CAPTION

FIGURE 1. Schemetic diagrams to present $\bar{x}$ as a function of β, showing five different cases which are possible, in the region III of Figure 2, for various values of the parameter β'. The dashed lines indicate unstable steady states, the solid lines indicate stable ones, while the closed dots indicate stable limit cycles. The dashed vertical line is the line $\beta = \beta'$, whose relative position gives rise to 10 possible types of phase space; A through J.

FIGURE 2. The graphs of equations (40) and (42) divide the (β, r_0) plane into 3 regions of different dynamic behavior. Here, $b = 1$, $d_0 = 0.3$, $d_1 = 0.01$, $\alpha = 0.9$, $\pi = 0.9$, $\gamma = 0.9$.

FIGURE 3. Numerical simulations of the model system (11)-(13). The parametric values are chosen so that a) $(\beta, r_0) = (0.4, 0.03)$ in Region I of Figure 2, where the solution trajectory is seen to approach the washout steady state, which is a saddle point, then gets repulsed. b) $(\beta, r_0) = (0.36, 0.5)$ in Region II, where the nontrivial steady state S is a stable spiral node, and c) $(\beta, r_0) = (0.55, 0.6)$ in Region III, where a limit cycle is observed as theoretically predicted.

FIGURE 4. The time series of the solutions to the model equations (11)-(13) in the cases a), b), and c) of Figure 3, respectively.

TABLE 1. Number of transients or attractors in each of the cases A through J as indicated in Figure 1.

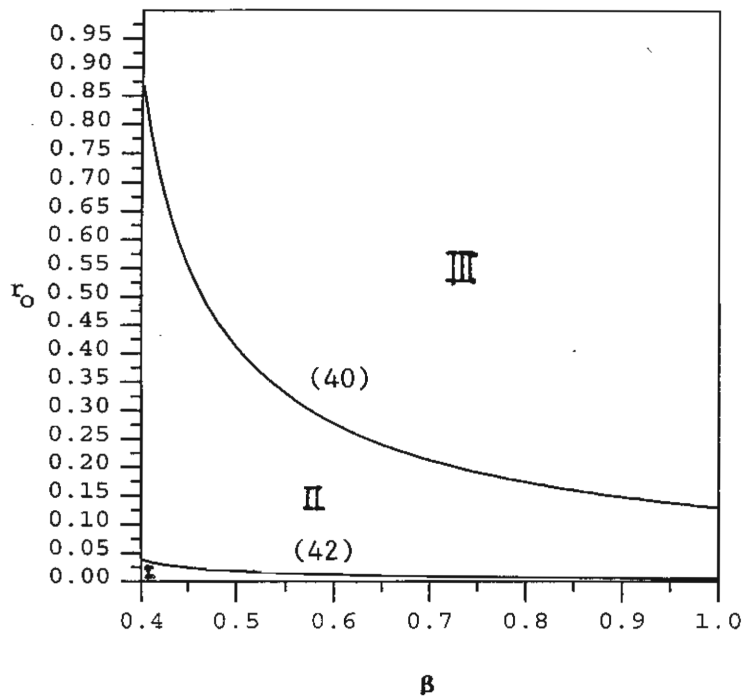
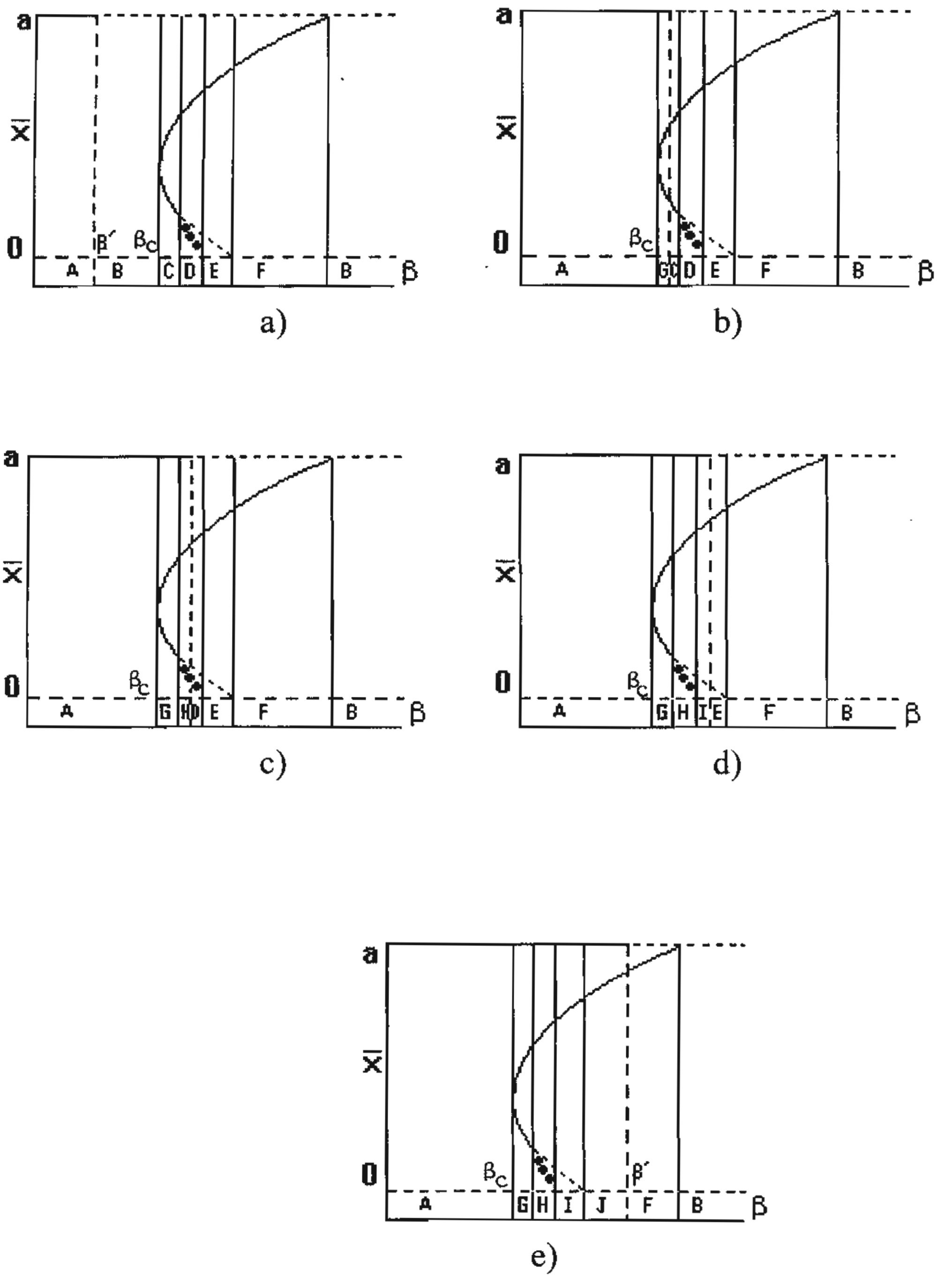
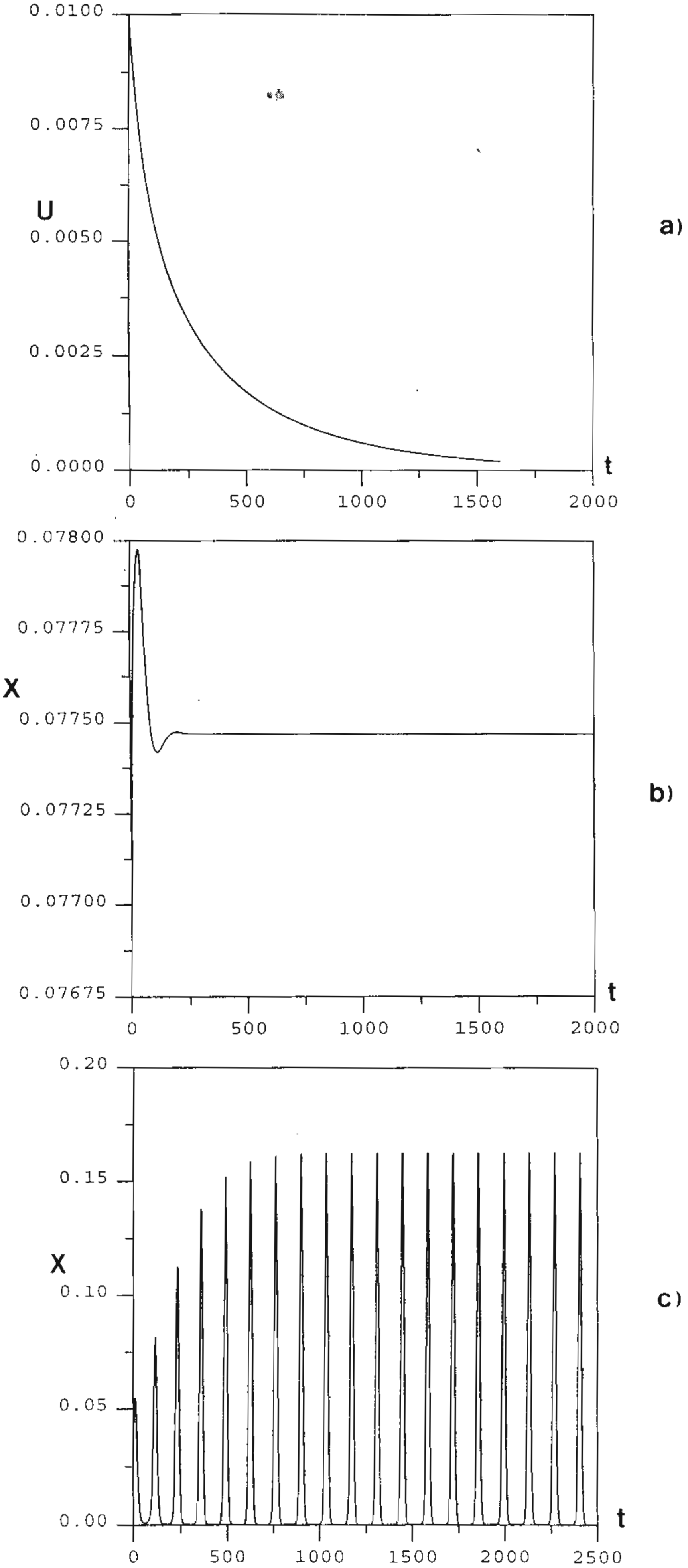

0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
r_o
III
(40)
II
(42)
I
0.4
0.5
0.6
0.7
0.8
0.9
1.0
β

FIG 1

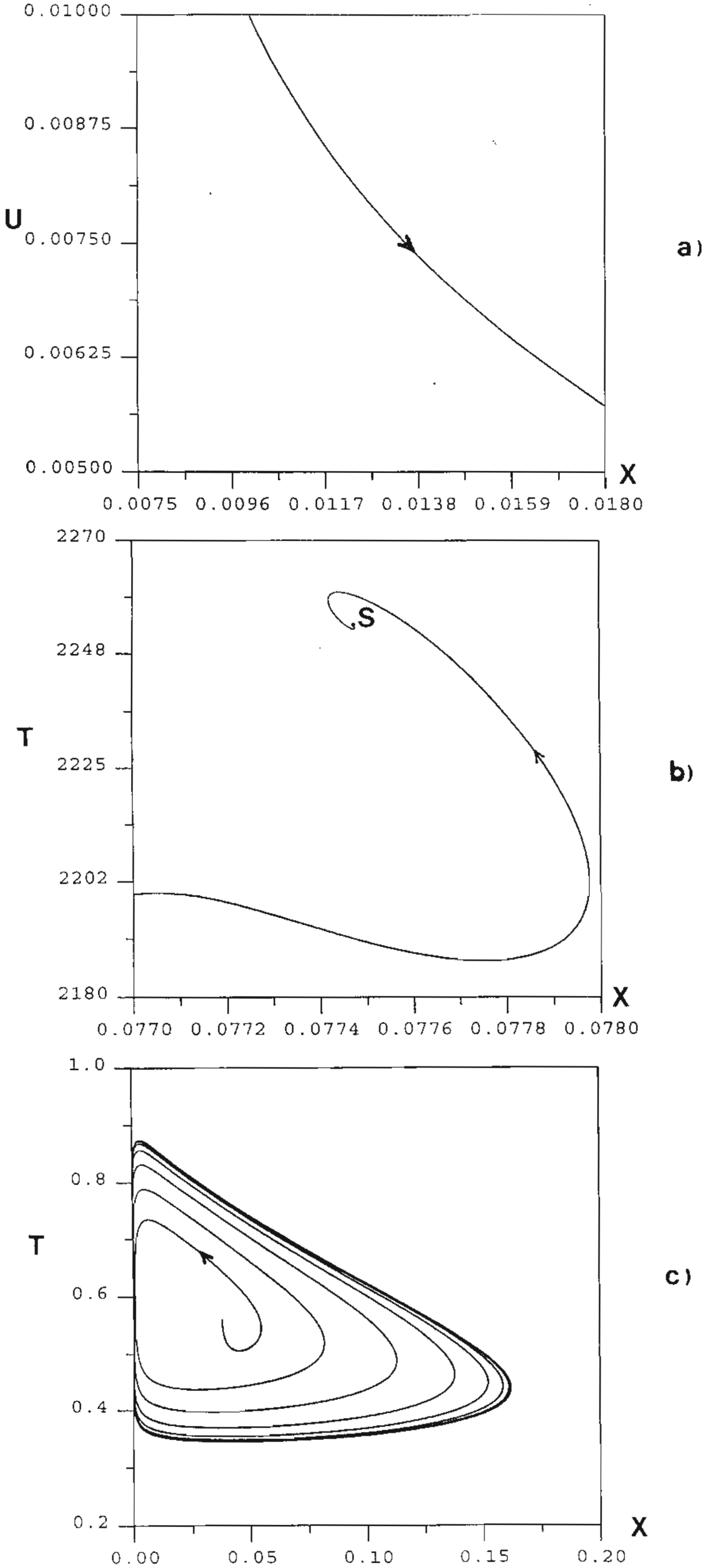


a
$\bar{X}$
0
β′
β_c
A B C D E F B
β
a)
a
$\bar{X}$
0
β_c
A G C D E F B
β
b)
a
$\bar{X}$
0
β_c
A G H D E F B
β
c)
a
$\bar{X}$
0
β_c
A G H I E F B
β
d)
a
$\bar{X}$
0
β_c
β′
A G H I J F B
β
e)

FIG. 2


0.0100
0.0075
U
0.0050
0.0025
0.0000
t
0
500
1000
1500
2000
a)
0.07800
0.07775
X
0.07750
0.07725
0.07700
0.07675
t
0
500
1000
1500
2000
b)
0.20
0.15
X
0.10
0.05
0.00
t
0
500
1000
1500
2000
2500
c)

FIG



0.01000
0.00875
U
0.00750
0.00625
0.00500
X
0.0075 0.0096 0.0117 0.0138 0.0159 0.0180
a)
2270
2248
T
2225
2202
2180
S
X
0.0770 0.0772 0.0774 0.0776 0.0778 0.0780
b)
1.0
0.8
T
0.6
0.4
0.2
X
0.00 0.05 0.10 0.15 0.20
c)

FIG.

สรุปและข้อเสนอแนะ

โครงการวิจัยนี้ได้บรรลุตามวัตถุประสงค์ที่เสนอไว้ ทั้งยังมีผลงานตีพิมพ์เผยแพร่ในวารสารมากกว่าจำนวนที่กำหนดไว้ในแบบเสนอโครงการ

ทั้งนี้ทุนที่ผู้วิจัยได้รับจาก สำนักงานกองทุนสนับสนุนการวิจัย เป็นแรงจูงใจและเกื้อหนุนอย่างดีเยี่ยมที่อำนวยให้ผู้วิจัยมีเวลาว่างจากภาระงาน และความรับผิดชอบด้านครอบครัวและเศรษฐกิจ และสามารถหันมาใช้เวลาอย่างจริงจังกับงานวิจัย จึงเป็นผลให้ผู้วิจัยมีผลงานลงตีพิมพ์เป็นจำนวนมากกว่าในอดีตที่ผ่านมา โดยที่ภายในระยะเวลา 3 ปี ของการรับทุนของ สำนักงานกองทุนสนับสนุนการวิจัย ผู้วิจัยสามารถมีผลงานตีพิมพ์ และเสนอในที่ประชุมนานาชาติรวม 10 ชิ้น ทั้งที่เกี่ยวกับโครงการนี้ และนอกเหนือไปจากงานวิจัยในโครงการ

อนึ่งการวิจัยทางด้านคณิตศาสตร์นั้นใช้งบประมาณด้านวัสดุน้อย เพียงแต่ใช้กระดาษ และดินสอก็จริง แต่จำเป็นต้องใช้เวลายาวนานในการคิดวิเคราะห์อย่างต่อเนื่อง จึงถือได้ว่าความสนับสนุนทางด้านเงินอุดหนุนค่าครองชีพจาก สำนักงานกองทุนสนับสนุนการวิจัย เป็นปัจจัยที่สำคัญยิ่งที่ผลักดันให้ผู้วิจัยได้มีผลงานวิจัยซึ่งมีจำนวนและคุณภาพที่สูงกว่าในอดีต

การวิเคราะห์วิจัยแบบจำลองทางคณิตศาสตร์ ซึ่งอธิบายปรากฏการณ์ในธรรมชาติที่เป็นระบบนิเวศวิทยาอันสำคัญ ทำให้เกิดความเข้าใจที่ดีขึ้นเกี่ยวกับระบบนั้น และเพิ่มขีดความสามารถให้แก่หน่วยงานที่เกี่ยวข้องกับปัญหาของสิ่งแวดล้อมทุกรูปแบบที่จะเกิดขึ้นอย่างเลี่ยงเสียมิได้ โดยผู้เกี่ยวข้องเหล่านี้จะสามารถแก้ไขปัญหาต่าง ๆ นั้นได้อย่างมีประสิทธิภาพ หรือสามารถปรับปรุงระบบการผลิตพันธุ์ต่าง ๆ ให้ได้ผลดียิ่งขึ้น ทั้งยังสามารถคิดค้นวิธีการ และเทคโนโลยีใหม่ ๆ ในการจัดการกับสภาพสิ่งแวดล้อมที่กำลังเสื่อมลง และพันธุ์พืชและสัตว์หลาย ๆ ชนิดที่กำลังจะสูญไป ปัญหาเหล่านี้ต้องการความเข้าใจที่ดี และสมควรต้องได้รับการศึกษาให้ลึกซึ้งอย่างต่อเนื่องต่อไป

สรุป Output ของโครงการ

Publication ในวารสารวิชาการระดับนานาชาติ

1 Lenbury, Y. and Orankitjaroen, S. Dynamic Behavior of Membrane Permeability Sensitive Model for a Continuous Bio-reactor Exhibiting Culture Rhythmcity. *J. Sci. Soc. Thailand.* **21** (1995) 97-114.

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4 Lenbury, Y. and Tumrasvin, N. Singular Perturbation Analysis of a Model for the Effect of Toxicant on a Single-Species System. *Mathl. and Comput. Modelling.* In press.

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1 Lenbury, Y., Puttapiban, P. and Amornsamarnkul, S. Modelling Effects of High Product and Substrate Inhibition on Oscillatory Behavior in Continuous Biorecators. *Mathematical Modelling of Systems.* Submitted.

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การเสนอผลงานในที่ประชุมวิชาการ

1 Lenbury, Y. How Can Nonlinear Dynamics Elucidate Mechanisms Relevant to Issues of Environmental Management and Global Change ? *The Second Asean Mathematical Conference*. Octorber 17-20, 1996. Suranaree University of Technology.

2 Lenbury, Y. Singular Perturbation Analysis of a Product Inhibition Model for Continuous Bio-Reactors. *International Conference on Dynamical Systems and Differential Equations*. May 29-June 1, 1994. Southwest Missouri State University, U.S.A.

3 Lenbury, Y. and Tumrasvin, N. Singular Perturbation Analysis of a Model for the Effect of Toxicant on a Single-Species System. *International Conference on Nonlinear Systems in Biology and Medicine*. July 17-20, 1996. Veszprem, Hungary.

ผลงานอื่น ๆ

1 สามารถผลิตบัณฑิตปริญญาโทสาขาคณิตศาสตร์ประยุกต์ให้สำเร็จการศึกษาไปแล้ว 2 คน โดยนักศึกษาทำงานวิจัยในโครงการนี้ แล้วนำผลการวิจัยเขียนขึ้นเป็นวิทยานิพนธ์

2 มีนักศึกษาปริญญาโทที่จะสำเร็จการศึกษาภายในปลายปี พ.ศ. 2540 อีก 2 คน

3 มีนักศึกษาสาขาคณิตศาสตร์ระดับปริญญาตรีที่ทำ senior project ร่วมในโครงการวิจัยนี้ และสำเร็จการศึกษาไปแล้ว 2 คน

เป็นการผลิตนักวิจัยรุ่นใหม่ให้กับวงการวิจัยด้านคณิตศาสตร์ประยุกต์ในประเทศ ระหว่างปี พ.ศ. 2538-2540 รวมทั้งสิ้น 6 คน (ปริญญาโท 4 คน, ปริญญาตรี 2 คน)

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2. Qualifications

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Ph.D. (Mathematics) Vanderbilt University, U.S.A., 1985.

3. Honours

1971-1977	Columbo Plan Scholarship, the Australian Government.
1975	The P. Bok Prize for the Best Female Science Student of the year, Australian National University.
1993	The Outstanding Research Work of the Year Award (in Physical Science), The National Research Council, Thailand.
1995-1996	Research Award, Thailand Research Fund.
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4. Experience

1 Dec. 1977 - 14 Sept. 1987	Lecturer, Department of Physic and Mathematics, Faculty of Science, Mahidol University.
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18 Dec. 1990 - Present	Assoc. Prof., Department of Mathematics, Faculty of Science, Mahidol University.
1990 - 1995	Chairman, Master of Science Program in Applied Mathematics.
1990 - 1994	Asst. Chairman, Department of Mathematics, Faculty of Science, Mahidol University.

5. List of Publications

1. Wiriyawit, Y., 1977, *Application of the Galerkin Method to Problems in Two Dimensional Compressible Fluid Flow* : M.Sc. Thesis.
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7. Research work presented in international conferences

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