

**THE INFLUENCE OF PESTS ON FOREST
AGE STRUCTURE DYNAMICS: THE
SIMPLEST MATHEMATICAL MODELS**

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PREFACE

Some of the most exciting current work in the environmental sciences involves unprecedentedly close interplay among field observations, realistic but complex simulation models, and simplified but analytically tractable versions of a few basic equations. IIASA's Environment Program is developing such parallel and complementary approaches in its analysis of the impact of environmental change on the world's forest systems. In this paper, Antonovsky, Kuznetsov and Clark provide an elegant global analysis of the kinds of complex behavior latent in even the simplest models of multiple-aged forests, their predators, and their abiotic environment. Subsequent papers will apply these analytical results in the investigation of case studies and more detailed simulation models.

I am especially pleased to acknowledge the important contribution made to the paper by Yuri Kuznetsov, a participant in IIASA's 1986 Young Scientist Summer Program and one of the 1986 Peccei award winners.

**R.E. Munn
Leader
Environment Program**

ABSTRACT

This paper is devoted to the investigation of the simplest mathematical models of non-even-age forests affected by insect pests. Two extremely simple situations are considered: 1) the pest feeds only on young trees; 2) the pest feeds only on old trees. It is shown that an invasion of a small number of pests into a steady-state forest ecosystem could result in intensive oscillations of its age structure. Possible implications of environmental changes on forest ecosystems are also considered.

SOFTWARE SUPPORT

Software is available to allow interactive exploration of the models described in this paper. The software consists of plotting routines and models of the systems described here. It can be run on an IBM-PC/AT with the Enhanced Graphics Display Adapter and 256K graphics memory.

For further information or copies of the software, contact the Environment Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria.

TABLE OF CONTENTS

Introduction	1
1. Results of the investigation of model (A.1)	3
2. Results of the investigation of model (A.2)	6
3. Discussion of the results	6
4. Summary	9
Appendix: Numerical procedures for the bifurcation lines R and P	
1. Andronov-Hopf bifurcation line R	11
2. Separatrix cycle line P	12
References	13

THE INFLUENCE OF PESTS ON FOREST AGE STRUCTURE DYNAMICS: THE SIMPLEST MATHEMATICAL MODELS

M.Ya. Antonovsky, Yu.A. Kuznetsov, and W. Clark

Introduction

The influence of insect pests on the age structure dynamics of forest systems has not been extensively studied in mathematical ecology.

Several papers (Antonovsky and Korzukhin, 1983; Korzukhin, 1980) have been devoted to modelling the age structure dynamics of a forest not affected by pests. Dynamical properties of insect-forest systems under the assumption of age and species homogeneity can be derived from the theoretical works on predator-prey system dynamics (May, 1981; Bazykin, 1985). In the present paper we attempt to combine these two approaches to investigate the simplest models of non-even-age forests affected by insect pests.

The model from Antonovsky and Korzukhin (1983) seems to be the simplest model of age structure dynamics of a one-species system. It describes the time evolution of only two age classes ("young" and "old" trees). The model has the following form:

$$\begin{cases} \dot{x} = \rho y - \gamma(y)x - fx \\ \dot{y} = fx - hy, \end{cases} \quad (\text{A.0})$$

where x and y are densities of "young" and "old" trees, ρ is fertility of the species, h and f are death and aging rates. The function $\gamma(y)$ represents a dependence of "young" trees mortality on the density of "old" trees. Following Antonovsky and Korzukhin (1983) we suppose that there exists some optimal value of "old" trees density under which the development of "young" trees goes on most success-

fully. In this case it is possible to choose $\gamma(y) = a(y - b)^2 + c$ (Figure 1). Let $s = f + c$.

Model (A.0) serves as the basis for our analysis. Let us therefore recall its properties. By scaling variables (x, y) , parameters (a, b, c, ρ, f, h, s) and the time, system (A.0) can be transformed into "dimensionless" form:

$$\begin{cases} \dot{x} = \rho y - (y - 1)^2 x - sx \\ \dot{y} = x - hy, \end{cases} \quad (0.1)$$

where we have preserved the old notations.

The parametric portrait of system (0.1) on the (ρ, h) -plane for a fixed s value is shown in Figure 2, where the relevant phase portraits are also presented.

Thus, if parameters (ρ, h) belong to region 2, system (0.1) approaches a stationary state with constant age classes densities (equilibrium E_2) from all initial conditions. In region 1 between lines D_1 and D_2 the system demonstrates a low density threshold: a sufficient decrease of each age class leads to degeneration of the system (equilibrium E_0). The boundary of initial densities that result in the degradation is formed by separatrices of saddle E_1 . Finally, in region 0 the stationary existence of the system becomes impossible.

Let us now introduce an insect pest into model (A.0). The two extremely simple situations seem to be possible:

- 1) the pests feed only on the "young" trees (undergrowth);
- 2) the pests feed only on the "old" (adult) trees.

Assume that in the absence of food the pest density exponentially declines and that forest-insect interactions can be described by bilinear terms as in the case of predator-prey system models (e.g., May, 1981; Bazykin, 1985).

Thus, for the case where the pest feeds on undergrowth we obtain the following equations:

$$\begin{cases} \dot{x} = \rho y - \gamma(y)x - fx - Axz \\ \dot{y} = fx - hy \\ \dot{z} = -\epsilon z + bzx, \end{cases} \quad (\text{A.1})$$

while for the case where the pest feeds on adult trees

$$\begin{cases} \dot{x} = \rho y - \gamma(y)x - fx \\ \dot{y} = fx - hy - Ayz \\ \dot{z} = -\epsilon z + byz. \end{cases} \quad (\text{A.2})$$

Here x is insect density, ϵ is mortality rate of insect, and terms with xz and yz represent the insect-forest interaction.

The goal of this paper is the comparative analysis of models (A.0), (A.1) and (A.2). In the final part of the paper we consider biological implications of the obtained results and outline possible directions for elaborating the model. The main tools for our investigation are the bifurcation theory of dynamical systems and the numerical methods of this theory.

1. Results of the investigation of model (A.1)

By a linear change of variables, parameters and time the system (A.1) can be transformed into the form:

$$\begin{cases} \dot{x} = \rho y - (y - 1)^2 x - sx - xx \\ \dot{y} = x - hy \\ \dot{z} = -\epsilon z + bzx, \end{cases} \quad (\text{1.1})$$

where the previous notations are preserved for new variables and parameters which have the same sense as in system (0.1).

In the first octant

$$\mathbb{R}_+^3 = \left\{ (x, y, z) : x, y, z \geq 0 \right\}$$

system (1.1) can have from one to four equilibria. The origin $E_0 = (0,0,0)$ is always an equilibrium point. On the invariant plane $z = 0$ at which the system coincides with system (0.1) there may exist either one or two equilibria with nonzero coordi-

nates. As in system (0.1), the two equilibria $E_1 = (x_1, y_1, 0)$ and $E_2 = (x_2, y_2, 0)$ where

$$y_{1,2} = 1 \pm \sqrt{\frac{\rho - sh}{h}}, \quad x_{1,2} = hy_{1,2},$$

appear in system (1.1) on the line:

$$D_1 = \left\{ (\rho, h) : \rho = sh \right\}.$$

On the line

$$D_2 = \left\{ (\rho, h) : \rho = (s + 1)h \right\},$$

equilibrium E_1 coalesces with equilibrium E_0 and disappears from \mathbb{R}_+^3 . Besides the equilibria $E_j, j=0,1,2$, system (1.1) could have an additional equilibrium

$$E_3 = \left\{ \frac{\varepsilon}{b}, \frac{\varepsilon}{bh}, \frac{\rho - sh}{h} - \left(\frac{\varepsilon}{bh} - 1 \right)^2 \right\}.$$

This equilibrium appears in \mathbb{R}_+^3 to the right of the line:

$$S = \left\{ (\rho, h) : \frac{\rho - sh}{h} - \left(\frac{\varepsilon}{bh} - 1 \right)^2 = 0 \right\},$$

passing through the plane $z=0$ and coalescing on this plane with either equilibrium E_1 or E_2 . Line S is tangent to line D_1 at point

$$M = \left(\frac{b}{\varepsilon}, \frac{b}{\varepsilon} \right)$$

and lies under it. Line S is divided by point M into two parts: S_1 and S_2 . Equilibrium E_3 collides on S_1 with E_1 and on S_2 with E_2 .

The parametric portrait of system (1.1) is shown in Figure 3, while the corresponding phase portraits are presented in Figure 4. In addition to the described bifurcations of the equilibria, autooscillations can "emerge" and "vanish" in system (1.1). These events take place on lines R and P on the parameter plane, while the autooscillations exist in regions 5 and 6.

Equilibrium E_3 loses its stability on line R due to the transition of two complex conjugated eigenvalues from the left to the right half-plane of the complex plane. This stability change results in the appearance of a stable limit cycle in system (1.1) (Andronov-Hopf bifurcation).

There is also a line corresponding to destruction of the limit cycles: line P on the (ρ, h) -plane. On line P a separatrix cycle formed by outgoing separatrices of saddles E_1 and E_2 does exist (Figure 5). While moving to the separatrix line the period of the cycle increases to infinity and at the critical parameter value it coalesces with the separatrix cycle and disappears.

The point M plays a key role in the parametric plane. This point is a common point for all bifurcation lines: S_1, S_2, D_1, D_2, R and P . It corresponds to the existence of an equilibrium with two zero eigenvalues in the phase space of the system. This fact allows us to predict the existence of lines R and P .

For parameter values close to the point M there is a two-dimensional stable-center manifold in the phase space of system (1.1) on which all essential bifurcations take place. The center manifold intersects with invariant plane $z=0$ along a curve. Thus we have a dynamical system on the two-dimensional manifold with the structurally unstable equilibrium with two zero eigenvalues and the invariant curve. This bifurcation has been treated in general form by Gavrilov (1978) in connection with another problem. It was shown that the only lines originating in point M are the mentioned bifurcation lines.

The locations of the R and P lines were found numerically on an IBM-PC/XT compatible computer with the help of standard programs for computation of curves developed in Research Computing Center of the USSR Academy of Sciences by Balabaev and Lunevskaya (1978). Corresponding numerical procedures are described in the Appendix. We have also used an interactive program for the integration of ordinary differential equations - PHASER (Kocak, 1986). On Figures 6, 7, and 8 the

changes in system behavior are visible.

2. Results of the investigation of model (A.2)

Model (A.2) can be transformed by scaling into the following form:

$$\begin{cases} \dot{x} = \rho y - (\gamma - 1)^2 x - sx \\ \dot{y} = x - h y - \gamma z \\ \dot{z} = -\varepsilon z + b \gamma z, \end{cases} \quad (2.1)$$

where the meaning of variables and parameters is the same as in system (1.1).

System (2.1) can have from one to four equilibrium points in the first octant \mathbf{R}_+^3 : $E_0 = (0,0,0)$, $E_1 = (x_1, y_1, 0)$, $E_2 = (x_2, y_2, 0)$ and $E_3 = (x_3, y_3, z_3)$. Equilibria E_1 and E_2 on the invariant plane $z = 0$ have the same coordinates as in system (1.1); they also bifurcate the same manner on lines D_1 and D_2 . As in system (1.1) there is an equilibrium point of system (2.1) in \mathbf{R}_+^3 :

$$E_3 = \left(\frac{\rho \varepsilon b}{(\varepsilon - b)^2 + s b^2}, \frac{\varepsilon}{b}, \frac{\rho b^2}{(\varepsilon - b)^2 + s b^2} - h \right).$$

This equilibrium appears in \mathbf{R}_+^3 below the line

$$S = \left\{ (\rho, h) : \frac{\rho b^2}{(\varepsilon - b)^2 + s b^2} - h = 0 \right\}.$$

But equilibrium E_3 does not lose its stability. Autooscillations in system (2.1) are therefore not possible. That is why the parametric portraits of system (2.1) look like Figure 9. Numbers of the regions in Figure 9 correspond to Figure 4.

3. Discussion of the results

The basic model (0.1) with two age classes describes either a forest approaching an equilibrium state with a constant ratio of "young" and "old" trees ($x = h y$), or the complete degradation of the ecosystem (and presumably, replacement by the other species).

Models (1.1) and (2.1) have regions on the parameter plane (0,1 and 2) in which their behavior is completely analogous to the behavior of system (0.1). In these regions the system either degenerates or tends to the stationary state with zero pest density. In this case the pest is "poorly adapted" to the tree species and can not survive in the ecosystem.

In systems (1.1) and (2.1) there are also regions (4 and 3) where the stationary forest state with zero pest density exists, but is not stable to small pest "invasions". After a small invasion of pests, the ecosystem approaches a new stationary state with nonzero pest density. The pest survives in the forest ecosystem.

The main qualitative difference in the behavior of models (1.1) and (2.1) is in the existence of density oscillations in the first system but not in the second one. This means that a small invasion of pests adapted to feeding upon young trees in a two-age class system could cause periodical oscillations in the forest age structure and repeated outbreaks in the number of pests (i.e., $x, y, x/y$ and z become periodic functions of time). It should be mentioned that the existence of such oscillations is usual for simple, even-aged predator-prey systems.

In our case, however, the "prey" is divided into interacting age classes and the "predator" feeds only on one of them. It is important that the pest invasions induce the oscillations in ratio x/y of the age classes densities. It should be mentioned also that in the case of model (2.1) the pest invasion can include damping oscillations in the age structure.

When we move on the parameter plane towards separatrix cycle line P , the amplitude of the oscillations increases and their period tends to infinity. The oscillations develop a strong relaxation character with intervals of slow and rapid variable change. For example, in the dynamics of the pest density $z(t)$ there appear periodic long intervals of almost zero density followed by rapid density outbreaks. Line P is a boundary of oscillation existence and a border above which a

small invasion of pests leads to complete degradation of the system. In regions 7 and 8 a small addition of insects to a forest system, which was in equilibrium without pests, results in a pest outbreak and then tree and pest death.

It can be seen that the introduction of pests feeding only upon the "young" trees dramatically reduces the region of stable ecosystem existence. The existence becomes impossible in regions 7 and 8.

We have considered the main dynamical regimes possible in models (1.1) and (2.1). Before proceeding, however, let us discuss a very important topic of *time scales* of the processes under investigation. It is well known that insect pest dynamics reflect a much more rapid process than the response in tree density. It seems that this difference in the time scales should be modeled by introduction of a small parameter $\mu \ll 1$ into the equations for pest density in systems (1.1) and (2.1): $\dot{z} \rightarrow \mu \dot{z}$. But it can be shown that the parametric portraits of the systems are robust to this modification. The relative positions of lines D_1, D_2 and S as well as the coordinates of the key point M depend on ratio ε/b which is invariant under substitutions $\varepsilon \rightarrow \varepsilon/\mu$, $b \rightarrow b/\mu$. The topology of the phase portraits is not affected by introduction of a small parameter μ , but in the variable dynamics there appear intervals of slow and rapid motions. Recall that in model (1.1) the similar relaxation character of oscillations was demonstrated near line P of separatrix cycle without additional small parameter μ . So we could say that we have an "implicit small parameter" in system (1.1).

To demonstrate the potential for extensions of this approach, let us now consider the qualitative implications of imposing on model (1.1) an effect of atmospheric changes on the forest ecosystems. As it was suggested in Antonovsky and Korzukhin (1983), an increase in the amount of SO_2 or other pollutants in the atmosphere could lead to a decrease of the growth rate ρ and an increase of the mortality rate h . Thus, an increase of pollution could result in a slow drift along some

curve on the (ρ, h) -plane (Figure 10).

Suppose that parametric condition has been moved from position 1 to position 2 on the plane but remains within the region where a stable equilibrium existence without pests is possible. But if the system is exposed to invasions of the pest it degrades on line P . Therefore, slow atmospheric changes could induce vulnerability of the forest to pests, and forest death unexpected from the point of view of the forest's internal properties.

4. Summary

It is obvious that both models (A.1) and (A.2) are extremely schematic. Nevertheless, they seem to be among the simplest models allowing the complete qualitative analysis of a system in which the predator differentially attacks various age classes of the prey.

The main qualitative implications from the present paper can be formulated in the following, to some extent metaphorical, form:

1. The pest feeding the young trees destabilizes the forest ecosystem more than a pest feeding upon old trees. Based upon this implication, we could try to explain the well-known fact that in real ecosystems pests more frequently feed upon old trees than on young trees. It seems possible that systems in which the pest feeds on young trees may be less stable and more vulnerable to external impacts than systems with the pest feeding on old trees. Perhaps this has led to the elimination of such systems by evolution.
2. An invasion of a small number of pests into an existing stationary forest ecosystem could result in intensive oscillations of its age structure.
3. The oscillations could be either damping or periodic.

4. Slow changes of environmental parameters are able to induce a vulnerability of the forest to previously unimportant pests.

Let us now outline possible directions for extending the model. It seems natural to take into account the following factors:

- 1) more than two age classes for the specified trees;
- 2) coexistence of more than one tree species affected by the pest;
- 3) introduction of more than one pest species having various interspecies relations;
- 4) the role of variables like foliage area which are important for the description of defoliation effect of the pest;
- 5) feedback relations between vegetation, landscape and microclimate.

Finally, we express our belief that careful analysis of simple nonlinear ecosystem models with the help of modern analytical and computer methods will lead to a better understanding of real ecosystem dynamics and to better assessment of possible environmental impacts.

Appendix: Numerical procedures for the bifurcation lines R and P

1. Andronov-Hopf bifurcation line R .

On the (ρ, h) -plane there is a bifurcation line R along which system (1.1) has an equilibrium with a pair of purely imaginary eigenvalues $\lambda_{1,2} = \pm i \omega$ ($\lambda_3 < 0$). It is convenient to calculate the curve R for fixed other parameter values as a *projection* on (ρ, h) -plane of a curve Γ in the direct product of the parameter plane by phase space \mathbb{R}_+^3 (Bazykin et al., 1985). The curve Γ in the 5-dimensional space with coordinates (ρ, h, x, y, z) is determined by the following system of algebraic equations:

$$\begin{cases} \rho y - (y - 1)^2 x - s x - x z = 0 \\ x - h y = 0 \\ -\varepsilon z + b x z = 0 \\ G(\rho, h, x, y, z) = 0, \end{cases} \quad (*)$$

where G is a corresponding Hurwitz determinant of the linearization matrix

$$A = \begin{pmatrix} (y - 1)^2 - s - z & \rho - 2(y - 1)x & -x \\ 1 & -h & 0 \\ bz & 0 & -\varepsilon + bx \end{pmatrix}.$$

Each point on curve Γ implies that at parameter values (ρ, h) a point (x, y, z) is an equilibrium point of system (1.1) (the first three equations of (*) are satisfied) with eigenvalues $\lambda_{1,2} = \pm i \omega$ (the last equation of (*) is satisfied).

One point on the curve Γ is known. It corresponds to point M on the parameter plane at which system (1.1) has the equilibrium $(\frac{\varepsilon}{b}, 1, 0)$ with $\lambda_1 = \lambda_2 = 0$ (e.g., $\pm i \omega = 0$). Thus, the point

$$(\rho^*, h^*, x^*, y^*, z^*) = \left(\frac{\varepsilon}{b}, \frac{\varepsilon}{b}, \frac{\varepsilon}{b}, 1, 0 \right)$$

lies on curve Γ and can be used as a beginning point for computations. The point-by-point computation of the curve was done by Newton's method with the help of a standard FORTRAN-program CURVE (Balabaev and Lunevskaya, 1978).

2. Separatrix cycle line P .

Bifurcation line P on the parameter plane was also computed with the help of program CURVE as a curve where a "split" function F for the separatrix connecting saddles $E_{2,1}$ vanishes:

$$F(\rho, h) = 0.$$

For fixed parameter values this function can be defined following Kuznetsov (1983). Let W_2^+ be the outgoing separatrix of saddle E_2 (the one-dimensional unstable manifold of equilibrium E_2 in \mathbb{R}_+^3). Consider a plane $z = \delta$, where δ is a small positive number; note the second intersection of W_2^+ with this plane (Figure 11). Let the point of intersection be X . The two-dimensional stable manifold of saddle E_1 intersects with plane $z = \delta$ along a curve. The distance between this curve and point X , measured in the direction of a tangent vector to the unstable manifold of E_1 , could be taken as the value of F for given parameter values. This function is well defined near its zero value and its vanishing implies the existence of a separatrix cycle formed by the saddle $E_{1,2}$ separatrices.

For numerical computations separatrix W_2^+ was approximated near saddle E_2 by its eigenvector corresponding to $\lambda_1 > 0$. The global part of W_2^+ was defined by the Runge-Kutta numerical method. Point X was calculated by a linear interpolation. The stable two-dimensional manifold of E_1 was approximated near saddle E_1 by a tangent plane, and an affine coordinate of X in the eigenbasis of E_1 was taken for the value of split function F .

The initial point on the separatrix has $z_0 = 0.005$. The plane $z = \delta$ was defined by $\delta = 0.1$ and the integration accuracy was 10^{-7} per step. The initial point on P was found through computer experiments. A family of the separatrix cycles corresponding to points on curve P is shown in Figure 12.

Figure 13 presents an actual parametric portrait of system (1.1) for $s = b = 1, \varepsilon = 2$.

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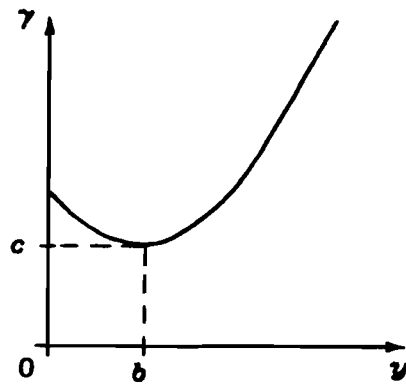


Figure 1. The dependence of "young" tree mortality on the density of "old" trees.

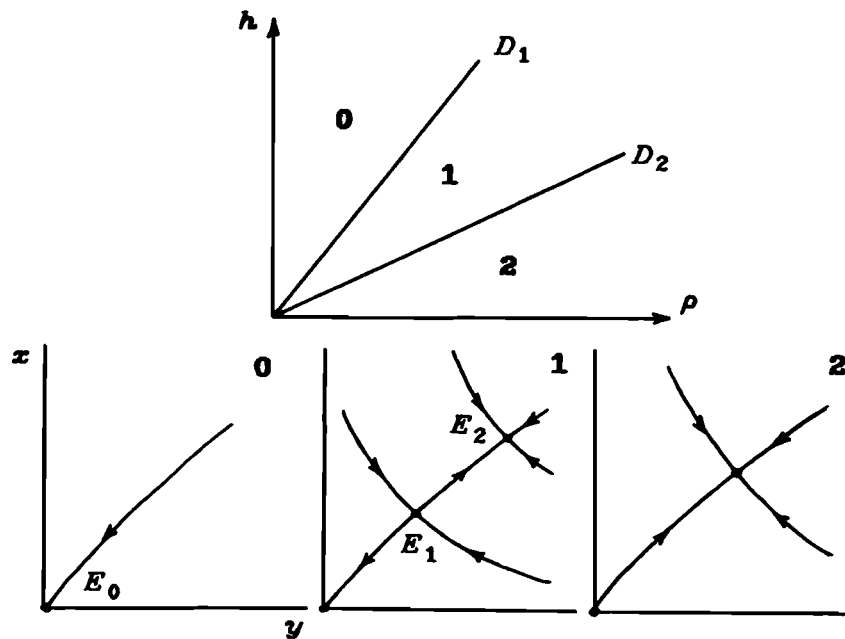


Figure 2. The parametric portrait of system (0.1) and relevant phase portraits.

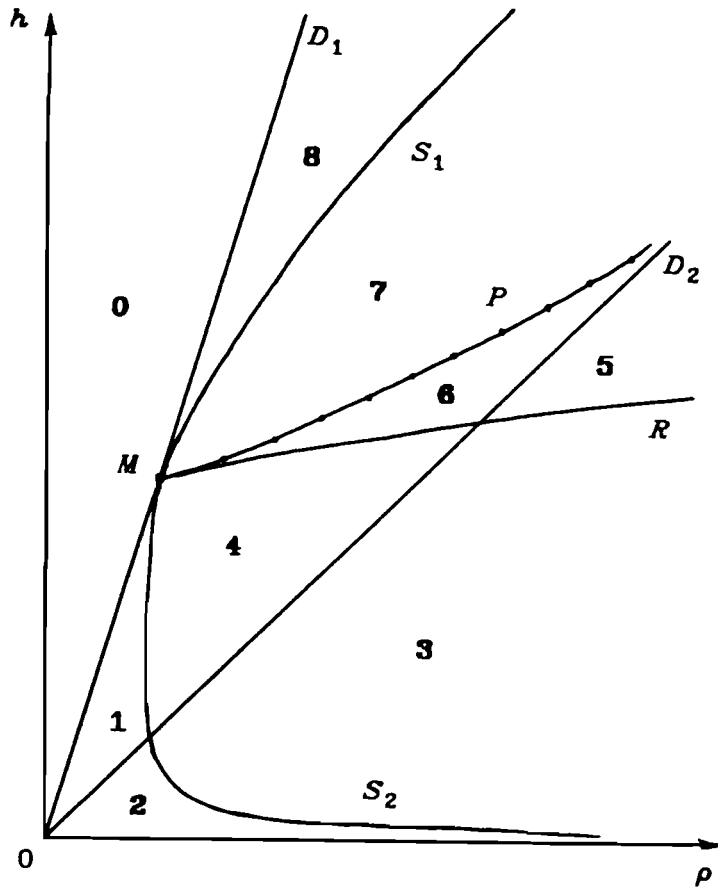


Figure 3. The parametric portrait of system (1.1).

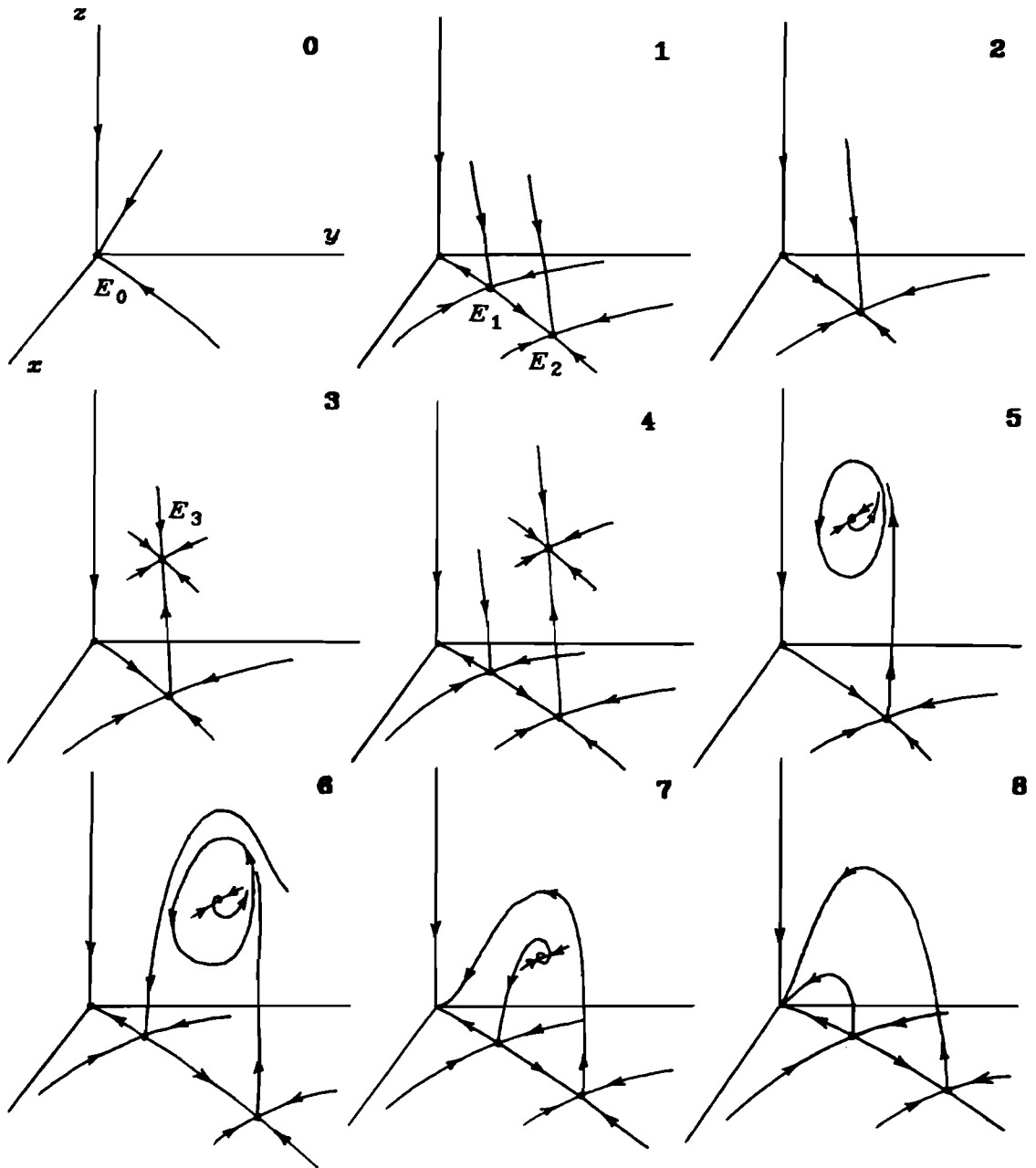


Figure 4. The phase portraits of system (1.1).

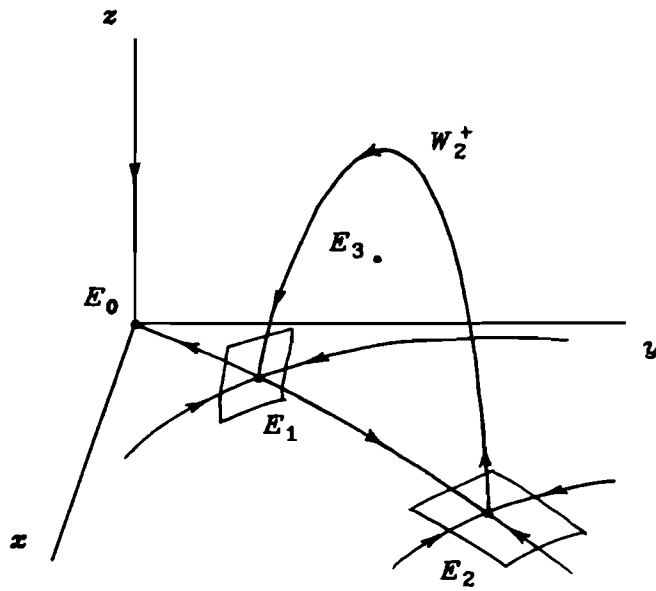


Figure 5. The separatrix cycle in system (1.1).

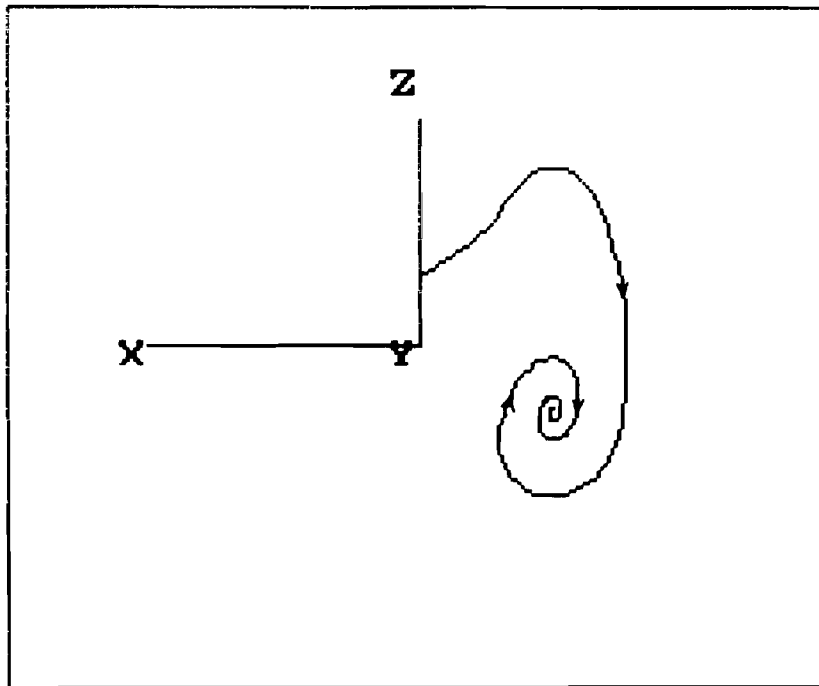


Figure 6. The behavior of system (1.1): $s = b = 1$, $\varepsilon = 2$, $\rho = 6$, $h = 2$ (region 3). The Y-axis extends vertically upward from the paper.

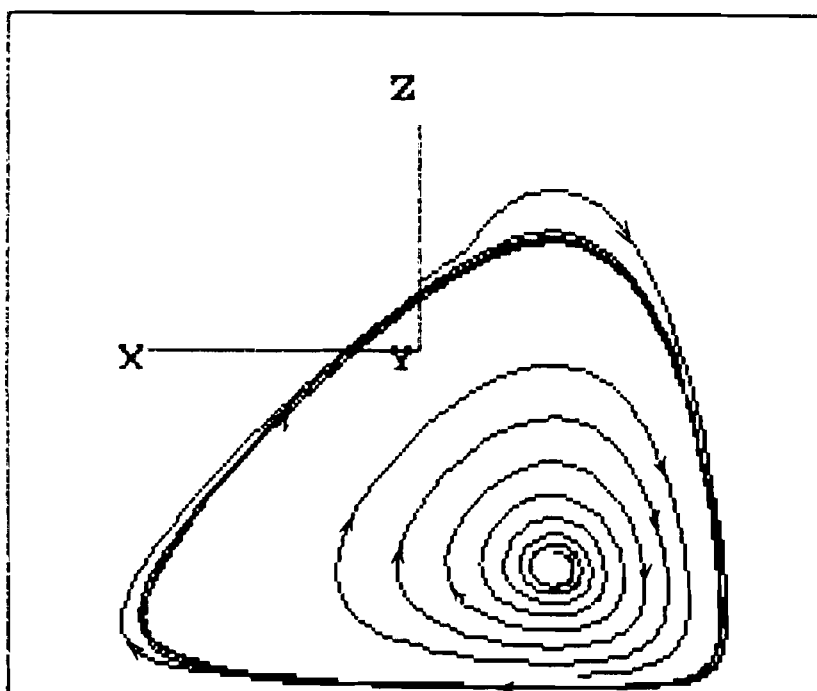


Figure 7. The behavior of system (1.1): $s = b = 1$, $\varepsilon = 2$, $\rho = 6$, $h = 3$ (region 6).

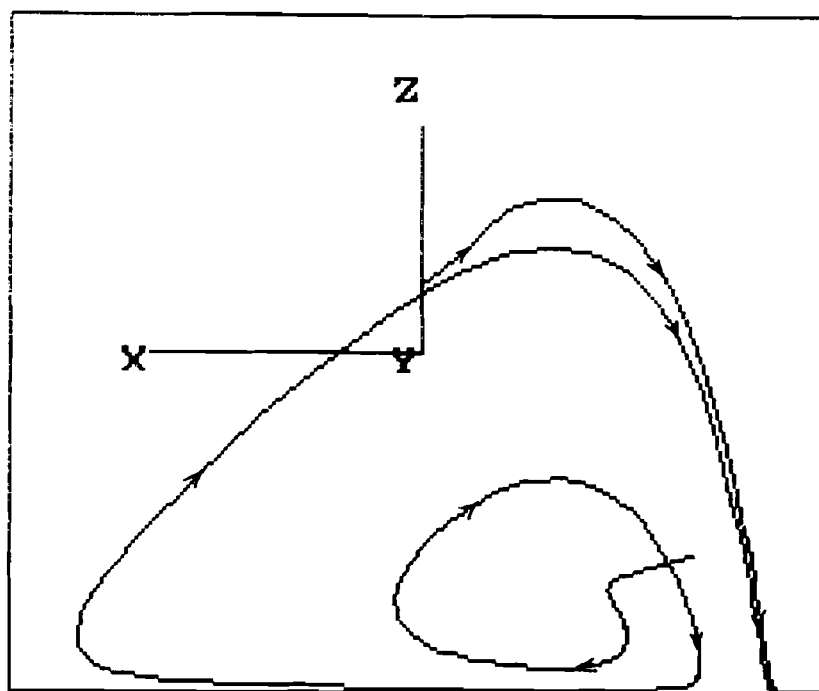


Figure 8. The behavior of system (1.1): $s = b = 1$, $\varepsilon = 2$, $\rho = 6$, $h = 3.5$ (region 7).

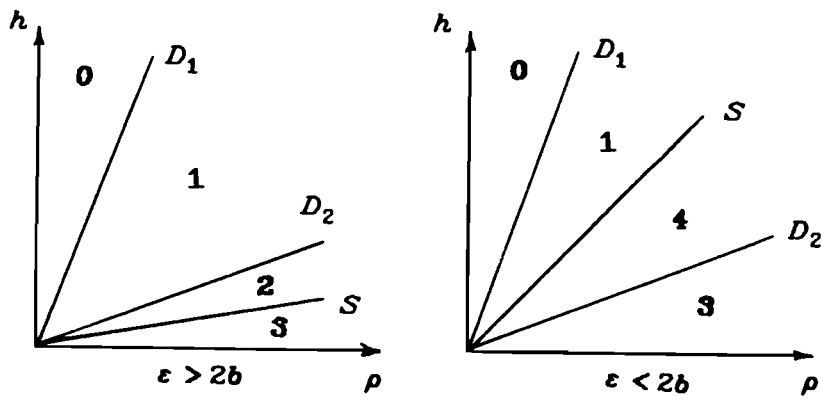


Figure 9. The parametric portraits of system (2.1).

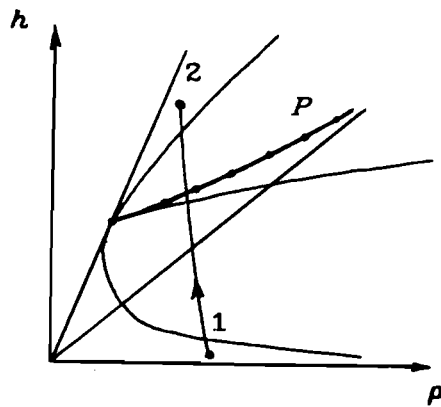


Figure 10. The probable parameter drift under SO_2 increase.

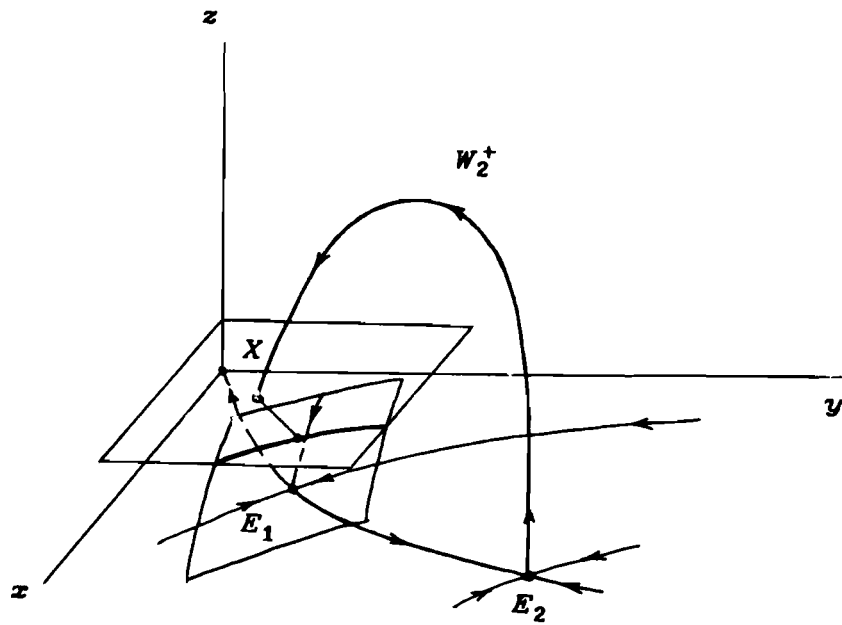


Figure 11. The separatrix split function.

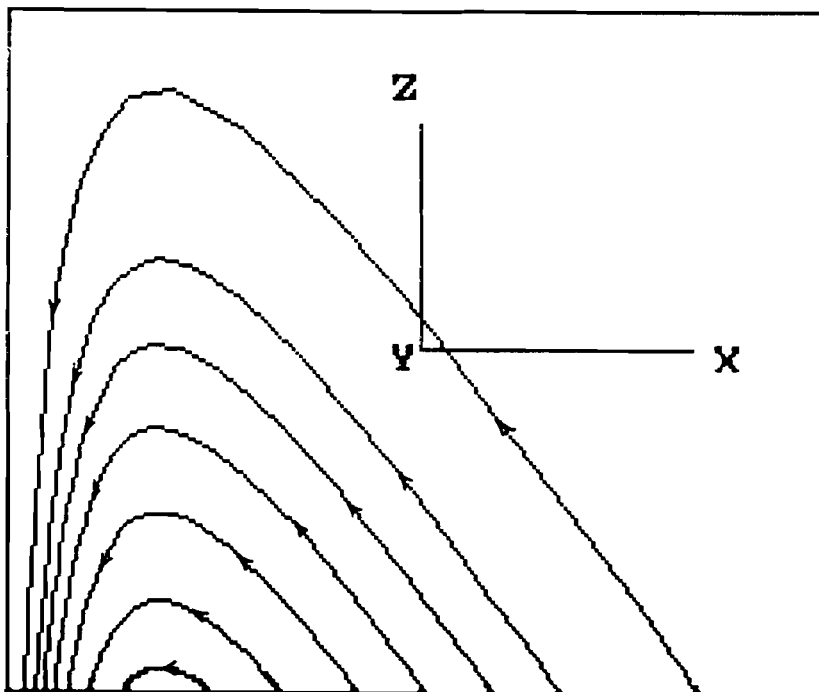


Figure 12. The separatrix cycles in system (1.1).

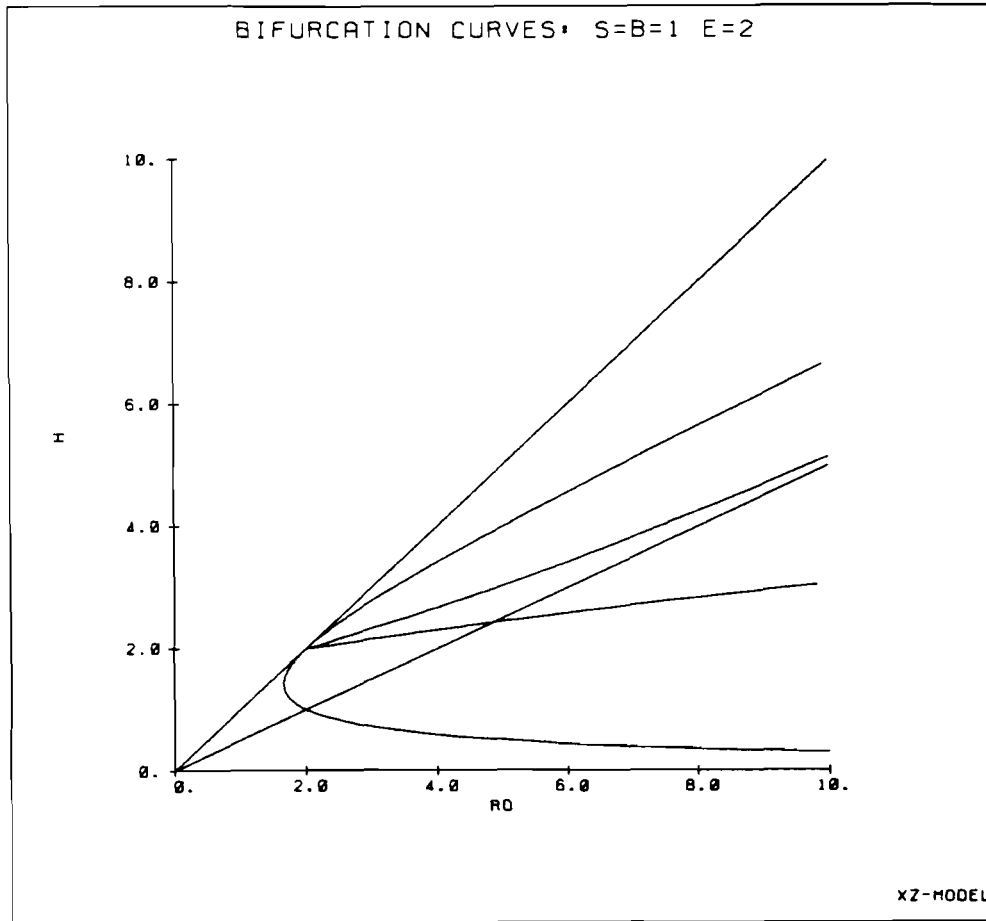


Figure 13. A computed parametric portrait of system (1.1).