Forest-Pest Interaction Dynamics: The Simplest Mathematical Models

M.Ya. Antonovsky
International Institute for Applied Systems Analysis
Laxenburg, Austria

R.A. Fleming
Forest Pest Management Institute, Forestry Canada,
P.O. Box 490, Sault Ste. Marie, Ontario, Canada P6A 5M7

Yu.A. Kuznetsov
Research Computing Centre, USSR Academy of Sciences,
Puscheno, USSR

W.C. Clark
Science and Public Policy Program,
J.F. Kennedy School of Government, Harvard University,
Cambridge, Massachusetts 02138

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Preface

The modeling of forest ecosystems is one of IIASA's continuous research activities in the Environment Program. There are two main approaches to this modeling: (a) simulation, and (b) qualitative (analytical). This paper belongs to the latter.

Analytical models allow the prediction of the behavior of key variables of ecosystems and can be used to organize and analyze data produced by simulation models or obtained by observations. This paper is devoted to the study of a simple mathematical model of spatially distributed non-even-age forests. The main tools used in the paper are new methods of qualitative theory of non-linear differential equations.

BO R. DÖÖS
Leader
Environment Program

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Forest–Pest Interaction Dynamics: The Simplest Mathematical Models[1]

M. YA. ANTONOVSKY

International Institute for Applied Systems Analysis,
A-2361 Laxenburg, Austria

R. A. FLEMING

Forest Pest Management Institute, Forestry Canada,
P.O. Box 490, Sault Ste. Marie, Ontario, Canada P6A 5M7

YU. A. KUZNETSOV

Research Computing Centre, USSR Academy of Sciences,
Puscheno, USSR

AND

W. C. CLARK

Science and Public Policy Program,
J. F. Kennedy School of Government, Harvard University,
Cambridge, Massachusetts 02138

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This paper is devoted to the investigation of the simplest mathematical models of non-even-aged 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. The parameter values of the second model are estimated for the case of balsam fir forests and the eastern spruce budworm. 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 in forest ecosystems are also considered. © 1990 Academic Press, Inc.

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[1] 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.

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1. INTRODUCTION

Although the influence of insect pests on the age structure dynamics of forest systems per se has not been extensively studied in mathematical ecology, there is a rapidly expanding literature on the more general problem of the stability of models with age-specific predation and parasitism. Gurtin and Levine (1979) showed that predation on only the youngest prey life stage can be destabilizing, but results since then are ambiguous. A number of more recent papers (e.g. Levine and Gurtin, 1981; Cushing and Saleem, 1982; Coleman and Frauenthal, 1983; Nunney, 1985; and Murdoch *et al.*, 1987) support Hastings' (1983, 1984) contention that age-dependent predation is not a simple process: model stability may be very sensitive to the way age structure is incorporated.

Several papers (e.g., 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. This paper is based upon IIASA WP–87–70 (Antonovsky *et al.*, 1987) and WP-87-71 (Fleming *et al.*, 1987).

The model from Antonovsky and Korzukhin (1983) is a simple 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 form

$$\begin{aligned} \dot{x} &= \rho y - \gamma(y)\, x - fx \\ \dot{y} &= fx - hy. \end{aligned} \tag{A.0}$$

where x and y are densities of "young" and "old" trees, ρ is the fertility of the species, and h and f are death and aging rates. The function $\gamma(y)$ represents a dependence of "young" tree mortality on the density of "old" trees. Following Antonovsky and Korzukhin (1983) we suppose that there exists some optimal value of "old" tree density under which the development of "young" trees goes on most successfully. In this case it is possible to choose $\gamma(y)=a(y-b)^2+c$ (Fig. 1).

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

$$\begin{aligned} \dot{x} &= py-(y-1)^2x-sx \\ \dot{y} &= x-hy, \end{aligned} \tag{0.1}$$

where we have preserved the old notations.

The parametric portrait of system (0.1) on the (p, h)-plane for a fixed s value is shown in Fig. 2. Relevant phase portraits are also presented there.

Thus, if parameters (p, h) belong to region 2, system (0.1) approaches a stationary state with constant age class 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 the 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) and consider two extremely simple situations:

(1) the pests feed only on the "young" trees (undergrowth);

(2) the pests feed only on the "old" (adult) trees.

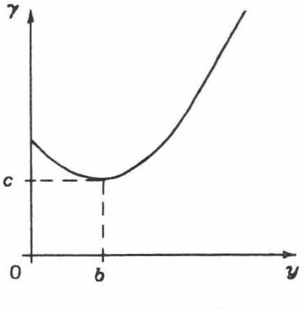

FIG. 1. The dependence of "young" tree mortality on the density of "old" trees.

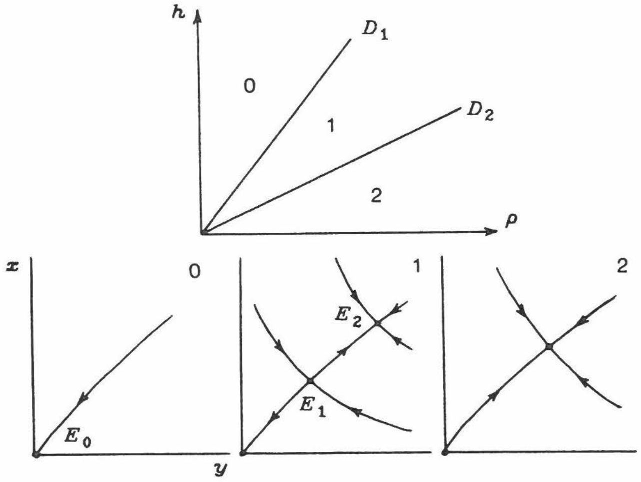

FIG. 2. The parametric portrait of system (0.1) and relevant phase portraits.

Assume that in the absence of food the pest density declines exponentially 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 equations

$$\begin{aligned} \dot{x} &= \rho y - \gamma(y)\,x - fx - Axz \\ \dot{y} &= fx - hy \\ \dot{z} &= -\varepsilon z + Bxz, \end{aligned} \tag{A.1}$$

while for the case where the pest feeds on adult trees we obtain the equations

$$\begin{aligned} \dot{x} &= \rho y - \gamma(y)\,x - fx \\ \dot{y} &= fx - hy - Ayz \\ \dot{z} &= -\varepsilon z + Byz. \end{aligned} \tag{A.2}$$

Here z is insect density, ε is the mortality rate of the insect, and the 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 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.

2. 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

$$\begin{aligned} \dot{x} &= \rho y - (y-1)^2 x - sx - xz \\ \dot{y} &= x - hy \\ \dot{z} &= -\varepsilon z + Bxz, \end{aligned} \tag{1.1}$$

where the previous notations are preserved for new variables and parameters which have the same sense as in system (0,1). The new parameters can be presented in terms of the old ones as

$$\rho := \frac{f\rho}{a^2b^4}, \qquad s := \frac{f+c}{ab^2}, \qquad h := \frac{h}{ab^2}, \qquad \varepsilon = \frac{\varepsilon}{ab^2}, \qquad B = \frac{B}{ab}.^2$$

In the first octant (i.e., where the variables take on biologically possible values),

$$\mathbf{R}^3_+ = \{(x, y, z) \colon x, y, z \geqslant 0\},$$

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 $z = 0$, where the system coincides with system (0.1), either one or two equilibria with nonzero coordinates may exist. As in system (0.1), the two equilibria $E_1 = (x_1, y_1, 0)$ and $E_2 = (x_2, y_2, 0)$, where

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

appear in system (1.1) on the line

$$D_1 = \{(\rho, h) \colon \rho = sh\}.$$

On the line

$$D_2 = \{(\rho, h) \colon \rho = (s+1)\, h\},$$

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

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

---

[2] $:=$ means that new variables were introduced but, for the sake of simplicity, the old notations were preserved: $f\rho/(a^2b^4) \to \rho$.

This equilibrium appears in $\mathbf{R}^3_+$ for parameter values (ρ, h) falling to the right of the line

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

in the parametric portrait (Fig. 3). E_3 passes through the plane $z=0$ and coalesces on this plane with either equilibrium E_1 or E_2 (Fig. 4). Line S is tangent to line D_1 at the point

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

in the (ρ, h)-plane. Line S is divided by point M into two parts, S_1 and S_2, on which equilibrium E_3 collides with either E_1 or E_2, respectively.

In addition to these bifurcations of the equilibria, autooscillations (i.e., neutrally stable oscillations) 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.

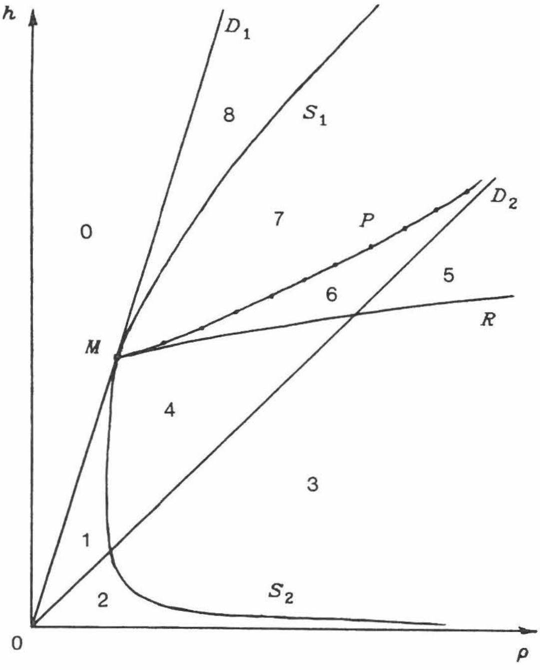

FIG. 3. The parametric portrait of system (1.1).

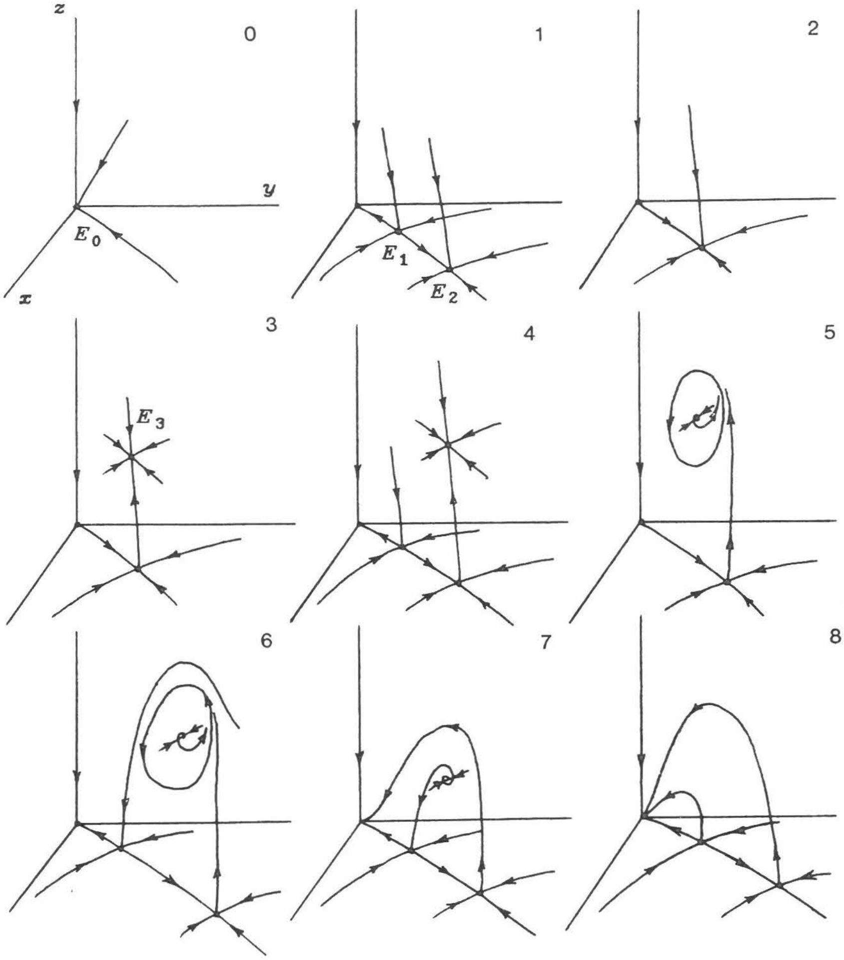

FIG. 4. The phase portraits of system (1.1).

Equilibrium E_3 loses its stability on line R due to the transition of two complex conjugate eigenvalues from the left to the right half 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 exists (Fig. 5). As the system approaches line P in parameter space (Fig. 3), the period of the limit cycle increases to infinity, and at the critical parameter value, the limit cycle coalesces with the separatrix cycle and disappears.

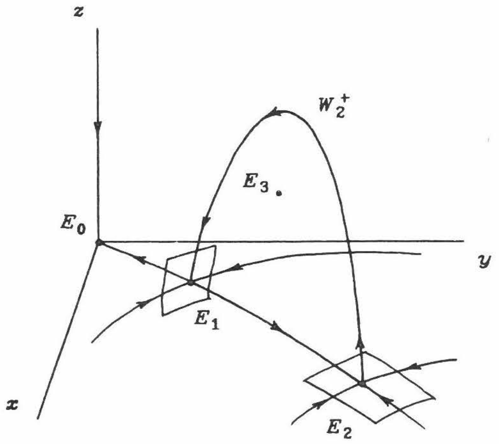

FIG. 5. The separatrix cycle in system (1.1).

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

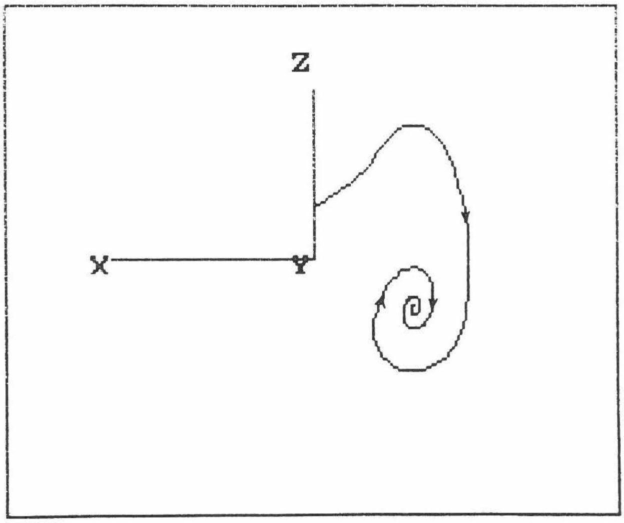

FIG. 6. The behavior of system (1.1): $s=b=1$, $\varepsilon=2$, $\rho=6$, $h=2$ (region 3). The Y-axis extends vertically upward from the paper.

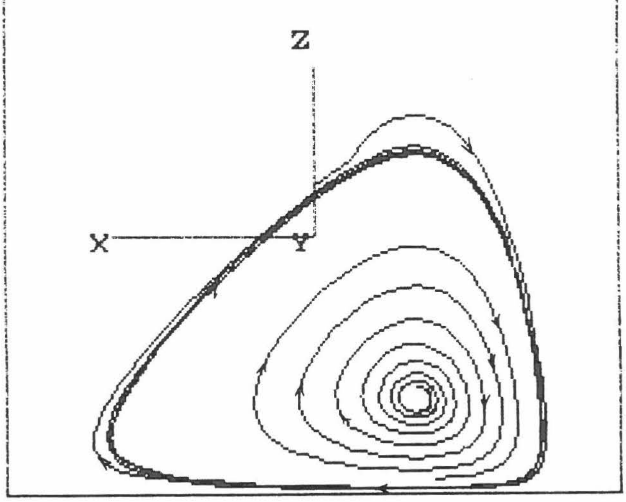

FIG. 7. The behavior of system (1.1): $s=b=1$, $\varepsilon=2$, $\rho=6$, $h=3$ (region 6).

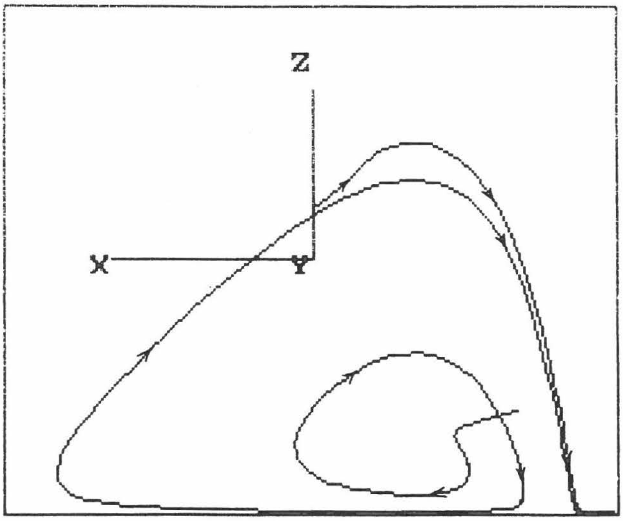

FIG. 8. The behavior of system (1.1): $s=b=1$, $\varepsilon=2$, $\rho=6$, $h=3.5$ (region 7).

invariant plane $z=0$ along a curve. Thus we have a dynamical system on the two-dimensional manifold with a 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 bifurcation lines mentioned above.

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 (Balabaev and Lunevskaya, 1978). The additional associated numerical procedures are described in the Appendix. We also used an interactive program for the integration of ordinary differential equations—PHASER (Kocak, 1986). Figures 6, 7, and 8 show the changes in system behavior as increases in h move the system through regions 3, 6, and 7.

3. RESULTS OF THE INVESTIGATION OF MODEL (A.2)

Model (A.2), which represents a pest attacking exclusively old trees, can be transformed by scaling into the form

$$\begin{aligned}\dot{x}&=\rho y-(y-1)^2 x-sx\\ \dot{y}&=x-hy-yz\\ \dot{z}&=-\varepsilon z+Byz,\end{aligned}\tag{2.1}$$

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 in 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 $\mathbf{R}^3_+$,

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

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

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

But equilibrium E_3 does not lose its stability, so autooscillations in

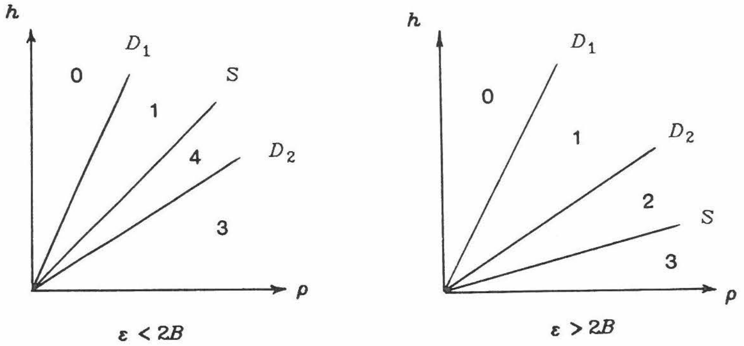

FIG. 9. The parametric portraits of system (2.1).

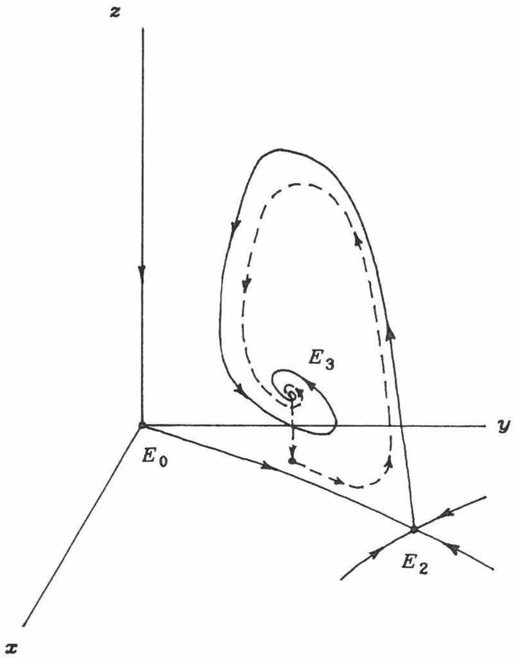

FIG. 10. A small decrease in the pest density may result in an insect population outbreak.

system (2.1) are not possible. Figure 9 shows the parametric portraits of system (2.1). The region numbers in Fig. 9 correspond to those in Fig. 4.

Consider in more detail the system behavior in parameter region 3 where damped oscillations are possible. In the absence of pests (i.e., $z = 0$) the system tends to equilibrium E_2 with constant densities of "young" and "old" trees. If a small number of pests then invades the forest, an outbreak occurs and the system moves to equilibrium E_3 with lower tree densities and a low density insect population. The maximum insect density reached during the outbreak exceeds that of equilibrium E_3.

A potentially unexpected system behavior can occur if the system is at equilibrium E_3 but the pest density then declines, perhaps due to pest control operations or the influence of random environmental variation. A new pest outbreak results (Fig. 10). Therefore, random declines in pest density may result in repeated outbreaks.

4. Parameter Estimation for Model (A.2)

Our goal here is to demonstrate how the model (A.2) might be applied to a real forest–pest ecosystem. This could lead to insight about the dynamics of the ecosystem or to a determination of the range of applicability of the model for describing ecosystem dynamics.

The eastern spruce budworm–forest system was picked as an appropriate candidate because of the availability of suitable information for many parts of the model, because of the similarity of the main model features to some key aspects of the budworm–forest system, and because previous models (e.g., Jones, 1979; Stedinger, 1984) of the budworm–forest system have emphasized different elements (e.g., foliage, insect predators, insect dispersal) of this system.

The eastern spruce budworm, *Choristoneura fumiferana* (Clem.), is a naturally occurring defoliator of balsam fir (*Abies balsamea* [L.] Mill.) in the boreal forests of eastern North America. Outbreaking populations kill their host trees over wide areas. Outbreak cycles range from 26–40 years in length with outbreaks lasting for 6–15 years. During outbreaks, insect numbers can increase over four orders of magnitude in stands of mature and overmature balsam fir, which are particularly vulnerable to attack.

In accordance with the simplistic nature of the model, which reduces the complex budworm–forest ecosystem to a system of three simultaneous differential equations, we take a "broad brush" approach to parameter estimation. First we identify realistic ranges for the parameter values and then we select from those ranges to see how well the model can simulate the behaviour of the ecosystem.

We begin by estimating h, the natural mortality rate of old trees in Eq. (A2). MacLean (1985) gives the "annual net probability of natural mortality (before outbreak)" as 1–3.8% for balsam fir. Hence, if n_a is the number of trees in a cohort of old trees of age a, then $n_{a+1} = n_a e^{-h}$, and $0.01 \leqslant (n_a - n_{a+1})/n_a \leqslant 0.038$. Hence

$$0.01 \leqslant h \leqslant 0.04 \text{ year}^{-1}. \tag{3.1}$$

The parameter f represents the aging of trees in the model. However, depending on how one defines "old" trees, f can take on different values. For instance, Bakuzis and Hansen (1965) report that balsam fir reaches sexual maturity at 30–35 years; becomes moderately susceptible to attack at over 40 years; and becomes very susceptible at over 60 years. Moreover, stands are generally 40–60 years of age when established seedlings first appear. Thus we assume that trees spend a mean duration of 30–70 years in the physiologically young age group. If this duration has an exponential distribution with a mean of 30–70 years, then

$$1/70 \leqslant f \leqslant 1/30$$

or

$$0.014 \leqslant f \leqslant 0.033 \text{ year}^{-1}. \tag{3.2}$$

The function $\gamma(y)$ describes the dependence of the natural mortality of young trees on y, the density of old trees. MacLean (1985) suggests that natural tree mortality might fall in the range 0.01–0.04 per year. Hence, since $c =$ minimum of $\gamma(y)$, we approximate

$$c = 0.01 \text{ year}^{-1}. \tag{3.3}$$

The increased mortality at low y (old tree density) could be ascribed to competition with ferns, shrubs, and hardwoods (Bakuzis and Hansen, 1965) invading sites opened up by the removal of the fir overstory. Competition with older trees accounts for the increase in young tree mortality at large y. Assuming that the interspecific competition is much less detrimental than the suppression by the older age group, then $b \ll y_{\max}$.

Taking $y_{\max} \approx 2.471$ (in units of 10^3 trees/ha) as indicating a fairly good site (Bakuzis and Hansen, 1965, Table 90), we arbitrarily set

$$b \simeq 0.1 \times y_{\max} \approx 0.2471 \text{ (in units of } 10^3 \text{ trees/ha)}. \tag{3.4}$$

Then, since $\gamma(y_{\max}) \simeq 0.04$ (MacLean, 1985).

$$\gamma_{\max} = a(y_{\max} - b)^2 + c \simeq 0.04.$$

Substituting (3.3), (3.4), and then solving for a.

$$a = 0.00606 \text{ (in units of ha}^2(10^3 \text{ trees})^{-2} yr^{-1}). \tag{3.5}$$

We have now estimated all the parameters of the forest section of the model (A.2) except ρ, the rate of production of seedlings. This parameter combines fertility, germination rate, and survivorship well past the first year of life (i.e., into the middle of the range of ages of the 'young' age group). Hence, it is a difficult parameter to estimate.

Our approach is to solve the system (A.2) for ρ using reasonable x and y values for the equilibrium without pests. For instance, $\dot{y} = 0$ in system (A.2) with $z = 0$ when $x = yh/f$. From $y_{\max} \simeq 2.471$, and from Bakuzis and Hansen (1965, Table 90), the corresponding value of x lies in the range 4.94–7.42 10^3 trees/ha. Hence, if we choose $f = 0.017 \text{ yr}^{-1}$ say (after Eq. (3.2)) and $h = 0.04 \text{ year}^{-1}$ (after Eq. (3.1)), then the value of x at the upper equilibrium (E_2 in Fig. 2) is approximately

$$x_{\max} = 5.81\ 10^3 \text{ trees/ha}.$$

Since this is a reasonable value of $x_{\max}$ (Bakuzis and Hansen, 1965, Table 90) we adopt

$$f = 0.017 \text{ year}^{-1} \tag{3.6}$$

and

$$h = 0.04 \text{ year}^{-1} \tag{3.7}$$

as reasonable initial guesses for these parameters.

For a forest equilibrium to occur near $(x_{\max}, y_{\max}) \simeq (5.81, 2.47)$ requires that the first equation in system (A.2) with $z = 0$ also meet equilibrium conditions at this point. Therefore, using (3.3)–(3.6),

$$\rho = 0.134 \text{ year}^{-1}. \tag{3.8}$$

This completes the estimation of parameters for the forest section of model (A.2) and leaves parameters ε, A, and B to be estimated. These three parameters represent the natural pest mortality and the interaction between the forest and the pest.

First we estimate ε, the instantaneous rate of pest mortality. After an outbreak there are often few mature and overmature balsam fir trees left. Hence, we assume y is small after an outbreak, so the pest equation in model (A.2) becomes $\dot{z} \simeq -\varepsilon z$. This equation has the solution $z_{t+1}/z_t \simeq e^{-t}$. Thus, after comparison it can be seen that ε corresponds to the negative part of the vertical axis of Royama's (1984) Fig. 8. From the minimum of his smooth eye-drawn curve we estimate

$$1 \leqslant \varepsilon \leqslant 1.5 \text{ year}^{-1}. \tag{3.9}$$

Next consider A, the instantaneous rate of tree mortality caused per pest. During outbreaks annual budworm-caused tree mortality peaks at 8–15% per year (MacLean, 1985). Hence, considering budworm-caused tree mortality in isolation, $\dot{y} = -Ayz$. Then, assuming z is relatively constant during the peak of an outbreak (Royama, 1984, Fig. 1), $y_{t+1}/y_t \approx e^{-Az}$. Hence, in analogy with the derivation of (3.1), $0.08 \leqslant 1 - e^{-Az} \leqslant 0.15$. Since z peaks on the order of

$$z_{\max} \simeq 20 \times 10^3 \text{ larvae/tree}$$

(Miller, 1975), this relationship becomes

$$0.00417 \leqslant A \leqslant 0.0081 \text{ in } 10^{-3} \text{ trees larvae}^{-1} \text{ year}^{-1}. \tag{3.10}$$

The per capita rate of pest increase per tree, B, remains to be estimated. When z is small and y is near its equilibrium density, y is relatively constant, so the pest equation in system (A.2) gives $z_{t+1}/z_t \approx e^{-(By-\varepsilon)}$. In analogy with the derivation of (3.9), we note that $(By - \varepsilon)$ corresponds to the positive vertical axis of Royama's (1984) Fig. 8. From the maximum of his curve we estimate

$$1 \leqslant By - \varepsilon \leqslant 2.$$

Since $y \approx y_{\max} \simeq 2.47$ and substituting (3.9),

$$0.8 \leqslant B \leqslant 1.42 \times 10^{-3} \text{ ha tree}^{-1} \text{ year}^{-1}. \tag{3.11}$$

The results of model (A.2), numerically integrated by a computer, are presented in Fig. 11. The parameters and initial conditions are chosen in accordance with Tables I and II. It can be seen that the chosen parameter values belong to region 3 on the right parameter portrait in Fig. 9, so an outbreak is expected. Computer simulation shows the outbreak has characteristics resembling aspects of real forest data. The outbreak length is about 15 years, which coincides well with observations (Royama, 1984). So the model, despite its extreme simplicity, could reproduce limited time series of a real outbreak and can be considered as a compressed representation of some aspects of available forest data.

There are two obvious differences between the computed outbreak shape and real budworm outbreaks. First, the time of intensive tree mortality is different. In the model this takes place at the peak of the outbreak, while

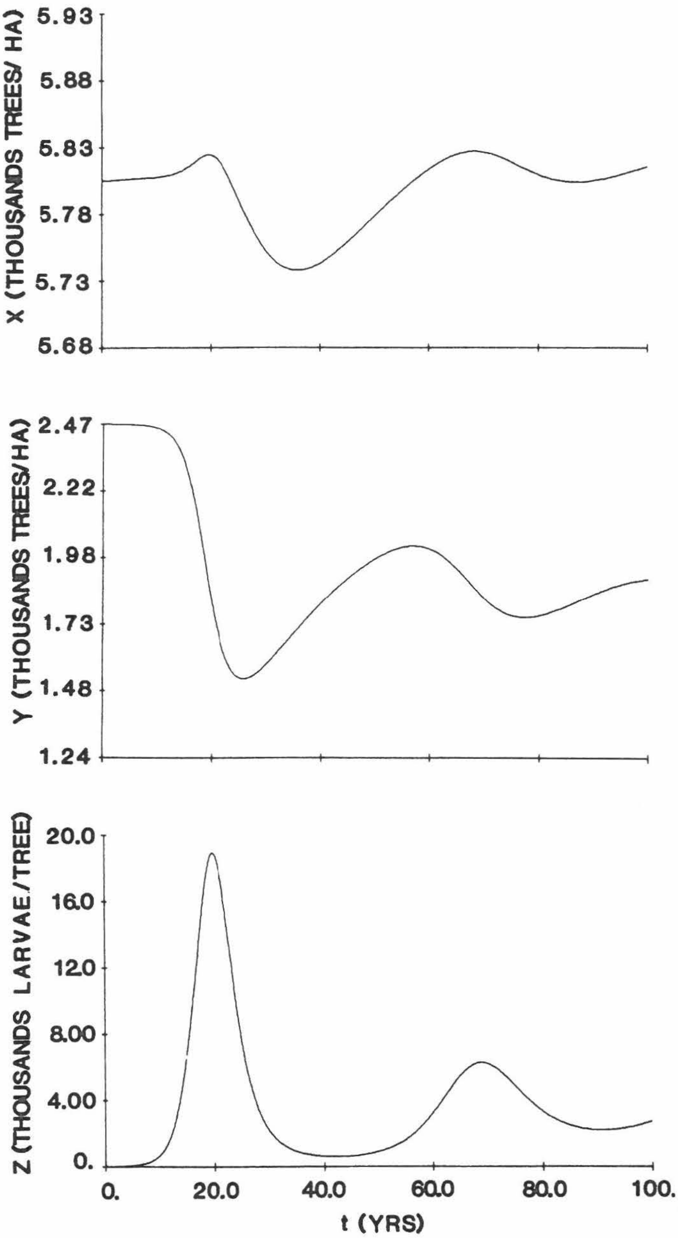

FIG. 11. An outbreak time equation.

TABLE I

Parameters for the Model

Parameter	Units	Range	Initial guess
a	$\mathrm{ha}^2(10^3\ \mathrm{trees})^{-2}\ \mathrm{yr}^{-1}$		0.00606
b	10^3 trees/ha		0.247
c	yr^{-1}		0.01
ρ	yr^{-1}		0.134
f	yr^{-1}	0.01–0.03	0.017
h	yr^{-1}	0.01–0.04	0.04
ε	yr^{-1}	1–1.5	1.5
A	10^{-3} trees $\mathrm{larvae}^{-1}\ \mathrm{yr}^{-1}$	0.004–0.008	0.004
B	10^{-3}ha $\mathrm{tree}^{-1}\ \mathrm{yr}^{-1}$	0.08–1.42	0.8

in the forest the mortality of trees comes after the insect population peaks. This may be the result of excluding consideration of foliage in the equations. In reality, the insects first defoliate trees and only then do trees begin to die due to defoliation. Nonetheless, this distinction is essentially a minor detail given the "broad brush" treatment of the problem employed here.

A more important problem with the model's behavior as far as representing budworm-forest dynamics is the inability of the modelled stand to fully recover after the initial outbreak. For instance, in simulated years 50–60, the density of old trees (y) peaks at about $\frac{3}{4}$ of its original ($t=0$) value. This behavior (damped oscillation) is determined by the model's structure and parameter values, which place the system (A.2) in phase portrait 3 of Fig. 4. An obvious question is whether random variation within the given ranges of parameter values (Table I), as might occur with changes in weather from year to year, could occasionally move the system into different phase portraits and thus maintain the oscillations.

Maintenance of the oscillations (perhaps as a limit cycle) might also be accomplished by a more accurate representation of the ecological processes considered in model (A.2). An obvious starting point here would be with

TABLE II

Initial Conditions

state variable	units	value
x (young trees)	10^3 trees/ha	5.81
y (old trees)	10^3 trees/ha	2.47
z (insect larvae)	10^3 larvae/tree	0.005

the term py. This term represents the rate of seedling establishment as a linear function of mature tree density. In fact, although a dense overstory of mature trees may produce many seeds, it can inhibit seedling establishment by limiting the available light. Hence, forest reproductivity, ρ, may be better described by a saturating function of mature tree density,

$$\rho(y) = [\rho^{-1} + y/(\dot{x}_{\max})]^{-1}.$$

Thus

$$\rho(y) \cdot y \begin{cases} \to \rho y & \text{when } y \text{ is small.} \\ \to \dot{x}_{\max} & \text{when } y \text{ is large.} \end{cases}$$

Here $\dot{x}_{\max}$, a constant, is the upper limit to seedling establishment when y is large.

5. 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 ($x = hy$), or degradation of the ecosystem (and, presumably, replacement by 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 cannot 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 models of even-aged predator–prey interactions.

In our case, however, the "prey" is divided into interacting age classes and the "predator" feeds only on one of them. It is the pest invasions which induce the oscillations in the ratio, x/y, of the age class densities.

Moreover, 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 toward 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 long periodic intervals of almost zero density followed by rapid density increases. 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 extinction.

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 we proceed, however, let us discuss the 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 the ratio ε/B, which is invariant under the substitutions $\varepsilon \rightarrow \varepsilon/\mu$, $B \rightarrow B/\mu$. The topology of the phase portraits is not affected by the introduction of a small parameter μ, but in the variable dynamics, intervals of slow and rapid motions appear. Recall that model (1.1) had oscillations of a similar relaxation character near line P of the separatrix cycle without any additional small parameter μ. So we could say that we have an "implicit small parameter" in system (1.1).

To demonstrate potential extensions of this approach, we now consider some qualitative implications that atmospheric change might have for forest–pest ecosystems. As suggested by 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, increases in atmospheric pollution could result in a slow drift along some curve on the (ρ, h)-plane (Fig. 12).

Suppose that the parametric condition has moved from position 1 to position 2 on the plane but remains in a region (8) where a stable equilibrium can exist without pests (Fig. 4). But now, if the system is exposed to pest invasions, both the forest and the pest become extinct. Therefore, slow atmospheric changes could induce both vulnerability of forests to

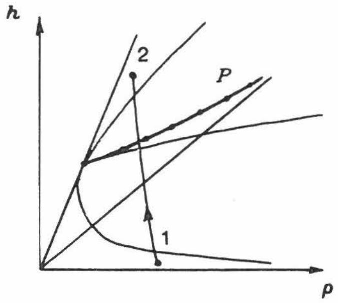

FIG. 12. The probable parameter drift under SO_2 increase.

pests, and forest death unexpected from the point of view of the forest's internal properties.

6. 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. An invasion of a small number of pests into an existing stationary forest ecosystem could result in intensive oscillations of the age structure of the tree population.
2. The oscillations could be either damping or periodic.
3. Slow changes of environmental parameters may make the forest vulnerable to previously unimportant pests.

There are a number of 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 which are important for describing the effect of defoliation by the pest;

(5) feedback relations between vegetation, landscape, and microclimate.

Finally, we express our belief that careful analysis of simple nonlinear ecosystem models will lead to a better understanding of real ecosystem dynamics and to a 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 other fixed parameter values as a *projection* on the (ρ, h)-plane of a curve Γ in the direct product of the parameter plane by phase space $\mathbf{R}^3_+$ (Bazykin *et al.*, 1985). The curve Γ in the 5-dimensional space with coordinates (ρ, h, x, y, z) is determined by the system of algebraic equations

$$\begin{aligned} \rho y - (y-1)^2 x - sx - xz &= 0 \\ x - hy &= 0 \\ -\varepsilon z + Bxz &= 0 \\ G(\rho, h, x, y, z) &= 0, \end{aligned} \tag{*}$$

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 $(\varepsilon/B, 1, 0)$ 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 the 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 $\mathbf{R}^3_+$). Consider a plane $z = \delta$, where δ is a small positive number; note the second intersection of W_2^+ with this plane (Fig. 13). 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

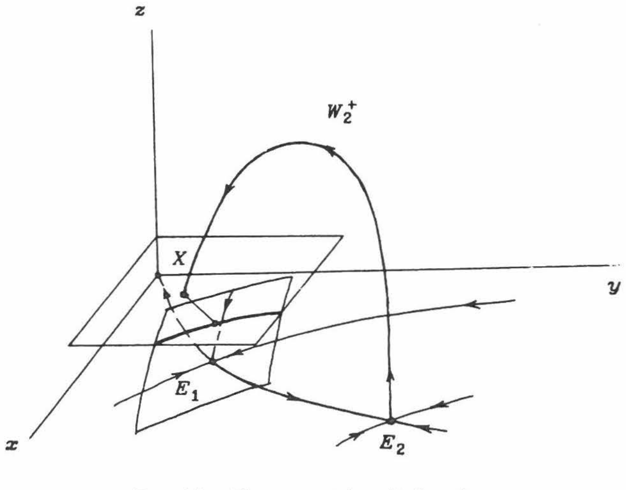

FIG. 13. The separatrix split function.

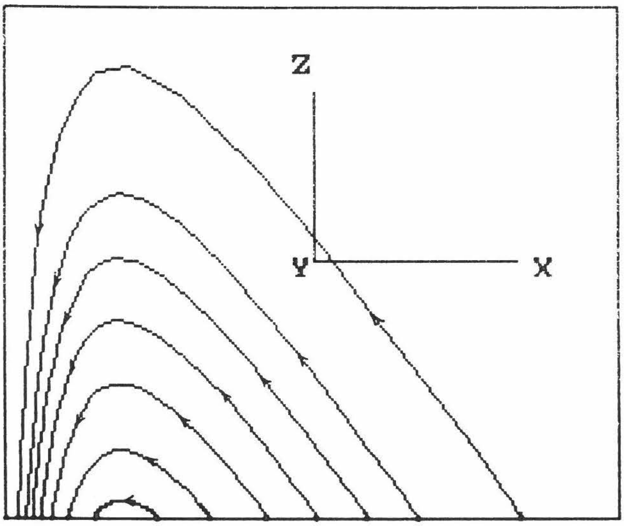

FIG. 14. The separatrix cycles in system (1.1).

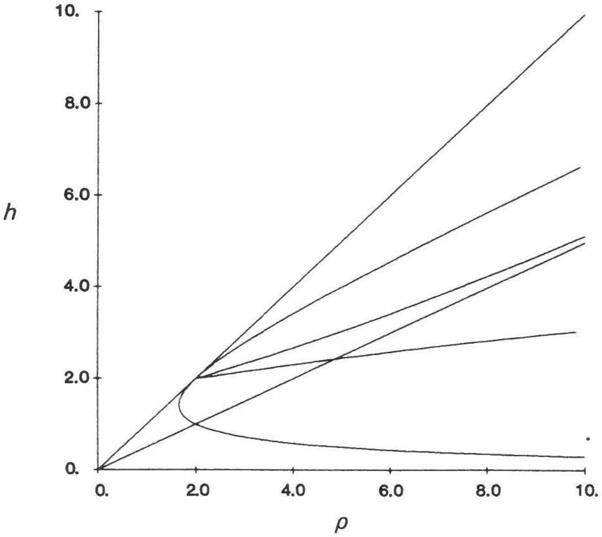

FIG. 15. A commuted parametric portrait of system (1.1).

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 Fig. 14.

Figure 15 presents an actual parametric portrait of system (1.1) for $s = B = 1, \varepsilon = 2$.

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