WORKING PAPER

SPATIAL-TEMPORAL STRUCTURE OF MIXED-AGE FOREST BOUNDARY: THE SIMPLEST MATHEMATICAL MODEL

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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.

This work is a continuation of the cooperation in forest modeling at IIASA started in 1986-89 by W. Clark, H. Shugart, R. Fleming and the authors of this paper.

Bo R. Döös
Environment Leader

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M.Ya.Antonovsky, E.A.Aponina and Yu.A.Kuznetsov**

1.INTRODUCTION

The modelling of forest age structure dynamics is one of the most important problems of mathematical ecology. Forest age structure dynamics is the variation of a tree number distribution in space and time caused by internal and external factors. In the previous papers (Antonovsky and Korzukhin, 1983; Korzukhin, 1980; Antonovsky et al. 1987,1988; Fleming et al., 1987), the simplest cases of mathematical models of non-even-age forests are considered. These models are based on a division of trees into age classes. For example, the original model proposed by Antonovsky and Korzukhin (1983) has the following form:

$$\begin{cases} \frac{du}{dt} = \rho v - \gamma(v)u - fu \\ \\ \frac{dv}{dt} = fu - hv \ , \end{cases} \tag{1}$$

where u and v are tree numbers (within some area) of "young" and "old" age classes respectively; ρ, f, h are coefficients of Leslie's matrix and $\gamma(v)$ is a mortality rate function of the "young" trees. It is assumed that there exists some optimal value of "old" tree density under which the recruitment of "young" trees is greatest. In this case, it is possible to chose $\gamma(v) = a(v-b)^2 + c$ with constant a,b,c.

Model (1) appears to describe the age dynamics of a small forest gap. In dimensionless variables it takes a form:

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$$\begin{cases} \dfrac{du}{dt} = \rho v - (v-1)^2 u - su \\ \\ \dfrac{dv}{dt} = u - hv \ . \end{cases} \tag{2}$$

Parameter and phase portraits of system (2) are presented in Figure 1. Two bifurcation lines for a fixed value of parameters have the following representations:

$$D_1 = \{(\rho,h)\colon \rho = sh\} \ , \ D_2 = \{(\rho,h)\colon \rho = (s+1)h\} \ .$$

In parameter region 1 between lines D_1 and D_2 a bi-stable behavior of the forest ecosystem is observed: depending upon the initial age structure the model forest either approaches a stable stationary state with some age class numbers u and v, or degenerates and replaces by a system without the trees.

In Korzukhin (1980) a generalization of model (1) was studied in which the existence of an intermediate age class was taken into consideration. Works by Antonovsky et al. (1987,1988) and Fleming et al. (1987) were devoted to the modelling of two age class forests affected by pests. These generalizations were still within a class of models that do not describe the spatial behaviour of the forest ecosystem.

However, it is known that real forest areas do have the age structure varying from one gap to the others. Local gaps are integrated into a joint forest ecosystem by various seed dispersion mechanisms and penetration of roots. In Samarskaya (1989) a problem of studying a spatially distributed ecosystem with local dynamics governed by (1) and its generalizations was stated. In the present paper, we use as a base model for qualitative description of a spatially distributed mono-species mixed-age forest the following generalization of model (1):

$$\begin{cases} \dfrac{\partial u}{\partial t} = \rho v - \gamma(v) u - fu + D \dfrac{\partial^2 u}{\partial x^2} \\ \\ \dfrac{\partial v}{\partial t} = fu - hv \ . \end{cases} \tag{3}$$

The diffusion term corresponds to various processes of "young" tree dispersion and has a phenomenological character. For a simplicity we have introduced only one space variable and assumed all parameters of (3) to be constants.

Using dimensionless variables we can write system (3) in the form:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \rho v - (v-1)^2\, u - su + \dfrac{\partial^2 u}{\partial x^2} \\[2ex] \dfrac{\partial v}{\partial t} = u - hv \; . \end{cases} \tag{4}$$

Equations (3) (and (4)) are nonlinear differential equations with partial derivatives of the "reaction-diffusion" type. We will assume in the following that local parameter values belong to region **1** of model (2) where the bi-stability is presented.

The main goal of this paper is to determine which kinds of solutions exist for model (4) and which processes in age structure dynamics the model describes.

2. STANDING FOREST BOUNDARY

The analysis of model (4) begins with spacially nonuniform stationary solutions: $u(x,t) = U(x)$, $v(x,t) = V(x)$. The solutions satisfy the system of two equations:

$$\begin{cases} \dfrac{d^2 U}{dx^2} + \rho V - (V-1)^2 U - sU = 0 \\ U - hV = 0 \; . \end{cases}$$

The second equation is algebraic and allows to find $U(x)$ if $V(x)$ is known: $U(x) = hV(x)$. That is why the problem of finding out stationary solutions of equations (4) reduces to the analysis of the equation:

$$hV'' + \rho V - h(V-1)^2 V - shV = 0 \; , \tag{5}$$

where $'$ denotes x-derivatives. Introducing a new variable, we can rewrite equation (5) as a system of two first order differential equations with "time" x:

$$\begin{cases} V' = W \\ W' = sV + (V-1)^2 V - \frac{\rho}{h} V \end{cases} \tag{6}$$

Bounded solutions of (6) define profiles of stationary solutions of system (4).

System (6) allows a complete qualitative analysis due to its Hamilton nature:

$$\begin{cases} V' = \dfrac{\partial H}{\partial W} \\ W' = -\dfrac{\partial H}{\partial V} \end{cases}$$

where

$$H(V,W) = \frac{1}{2}(W^2 + \frac{\rho - (s+1)h}{h} V^2) - \frac{V^4}{4} + \frac{2V^3}{3} . \tag{7}$$

In parameter region 1 between lines D_1 and D_2 system (6) has phase portraits presented in Figure 2. Equilibria in system (6) have the following coordinates:

$$E_o = (0,0), \; E_{1,2} = (V_{1,2}^0, 0) ,$$

where $V_{1,2}^o = 1 \pm \sqrt{\frac{\rho - sh}{h}}$.

Equilibria E_o and E_2 are saddles while equilibrium E_1 is a center. Bounded nontrivial trajectories of system (6) are either closed or connect saddles. It follows from H-isoline analysis.

The closed trajectories of system (6) correspond to stationary space-periodic solutions of system (4) which describe periodic space distributions of tree age. The separatrix connecting a saddle with itself corresponds to stationary maximum or minimum in the tree densities. The most interesting solution corresponds to a separatrix connecting two saddles. For example, a separatrix going from saddle E_o to saddles E_2 corresponds to a solution of system (4) which has a shape of a stationary front. The front connects nontrivial stable forest state with stable degenerate state and may be treated as a simple mathematical image of a mono-species mixed-age forest boundary (Figure 3). The equation of line Q on which a separatrix connecting saddles E_o and E_2 exists in system (6) may be found analytically from the condition that isoline $H = 0$ goes through saddle E_2:

$$Q = \{(\rho,h)\colon \rho = (s+\frac{1}{9})h\} .$$

Therefore, we have established a possibility for existence of a standing space boundary of the forest modeled by system (4) but only for the specific relation between parameters (ρ,s,h).

3. TRAVELING FOREST BOUNDARY

Let us consider a problem of existence of nonuniform solutions of (4) which are traveling waves propagating with a constant speed:

$$u(x,t) = U(x+ct),\ v(x,t) = V(x+ct) ,$$

where c is a propagation speed. These solutions satisfy the following equations:

$$\begin{cases} c\,\dfrac{dU}{d\xi} = \rho V - (V-1)^2\, U - sU + \dfrac{d^2U}{d\xi^2} \\ c\,\dfrac{dV}{d\xi} = U - hV , \end{cases}$$

where $\xi = x + ct$. Introducing a new variable $W = \dfrac{dU}{d\xi} \equiv U_\prime$, we obtain a system of three differential equations of the first order

$$\begin{cases} U' = W \\ W' = cW - \rho V + (V-1)^2 U + sU , \\ V' = \dfrac{1}{c}(U-hV) \end{cases} \tag{8}$$

where ξ plays a role of "time".

Bounded solutions of (8) define profiles of traveling waves in system (4).

Equilibria of system (8) in parameter region 1 do not depend on c value and are located in the plane $W=0$ with coordinates:

$$E_o=(0,0,0),\ E_{1,2}=(hV^0_{1,2},\ O,V^0_{1,2})\ .$$

Linearization matrix of (8),

$$A=\begin{bmatrix} 0 & 1 & 0 \\ (V-1)^2+s & c & 2(V-1)U-\rho \\ 1/c & 0 & h/c \end{bmatrix}$$

has at points E_o and E_2 two eigenvalues with negative real parts and a positive eigenvalue:

$$\mathrm{Re}\ \lambda_{1,2}(E_j)<0,\ \ \lambda_3(E_j)>0,\ \ j{=}0,2,$$

for all parameters from region 1. Equilibria E_o and E_2 in system (8) are therefore topological saddles with one dimensional unstable invariant manifolds $W^u(E_j)$ and two dimensional stable manifolds $W^s(E_j)$. The unstable manifold of E_j is formed by two outgoing from E_j trajectories: Γ_{j1}, Γ_{j2}. The stable manifold of E_j is formed by all ingoing trajectories (Figure 4).

If there are parameter values for which system (8) has a separatrix going from one saddle to the other then for these parameter values (ρ,s,h,c) system (4) should have a traveling wave front (Figure 5). For fixed parameter values (ρ,s,h) traveling front could have only isolated propagation speeds.

Calculations by Interactive Integator TraX developed in the Research Computing Centre of the USSR Academy of Sciences (Pushchino, Moscow region) can be used to display separatrix Γ_{01} of saddle E_o going to saddle E_2. For $\rho{=}6$, $s{=}1$, $h{=}4$ the behavior of separatrix Γ_{01} is presented in Figure 6 for two values of parameter c : $c_1=$ .560 and $c_2=0.565$. Hence, there is a value of speed c : $c_1<c<c_2$, for which separa-

trix Γ_{01} connects the saddles.

Let $F(\rho,s,h,c)$ be a "split function" for invariant manifolds of saddles E_0 and E_2 (Kuznetsov, 1983). Fix parameters s and c. Then equation $F(\rho,s,h,c) = 0$ defines a curve of constant speed front propagation on (ρ,h)-plane. Several curves c = constant are presented in Fig.7. With an unexpected accuracy the curves may be approximated by straight lines (see also Table 1). A hypothesis is that they are straight lines for model (4).

Therefore, an existence of a traveling forest boundary is found within model (4) and the speed of boundary propagation is calculated.

4. DISCUSSION

Summarizing the results from parts 2 and 3, it is possible to make an implication that model (3) of mono-species mixed-age forest has a complex space-time behavior.

Model (3) predicts a possibility of existence of stationary or traveling forest boundary from one side of which the modelled forest demonstrates an equilibrium state with nonzero age class densities, while from the other side there are no trees of the studied type. The stationary boundary exists only for special parameter values (on line Q). For other parameter values from region **1** the boundary becomes propagating which is possible in both directions along x-axis.

Parameter values (ρ,s,h) are determined by internal forest ecosystem properties and by external impacts (for example, SO_2 concentration in the atmosphere). It is possible, therefore, the following behaviour of the forest boundary caused by increase of tree mortality rate h due to some antropogenic impacts. For an initial parameter value h, there may exist a wave front with positive speed. In this case the area of a modelled forest grows. With the increase of h the boundary speed decreases and after crossing line Q a front of forest degradation (negative speed) is observed and the forest area decreases. Hence, global atmospheric changes can lead to deforestation by indirect impact on internal forest population dynamics.

The problem of traveling boundary stability needs special study. The stability of asymptotic equilibria connected by the front is only a necessary condition for its stability as a solution of partially differential equations (3).

Finally, we should point out that a main goal of this paper is to stress the importance of spatial effects for studying forest ecosystem's output to external impacts and to demonstrate a usefulness of a qualitative model approach to this problem.

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Table 1: The line of constant propagation speed $c = 0.5$ for $s = 1$ in system (4).

ρ	h
1.6	0.777
2.0	1.100
3.0	1.884
3.5	2.270
4.0	2.655
4.5	3.038
5.0	3.420
5.5	3.801
6.0	4.182
6.5	4.562
7.0	4.942
10.0	7.217

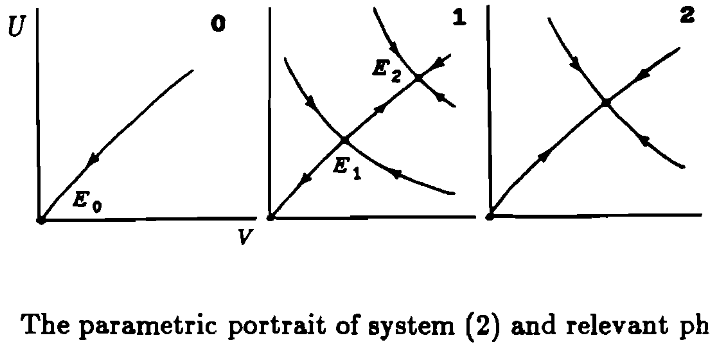

Figure 1: The parametric portrait of system (2) and relevant phase portraits.

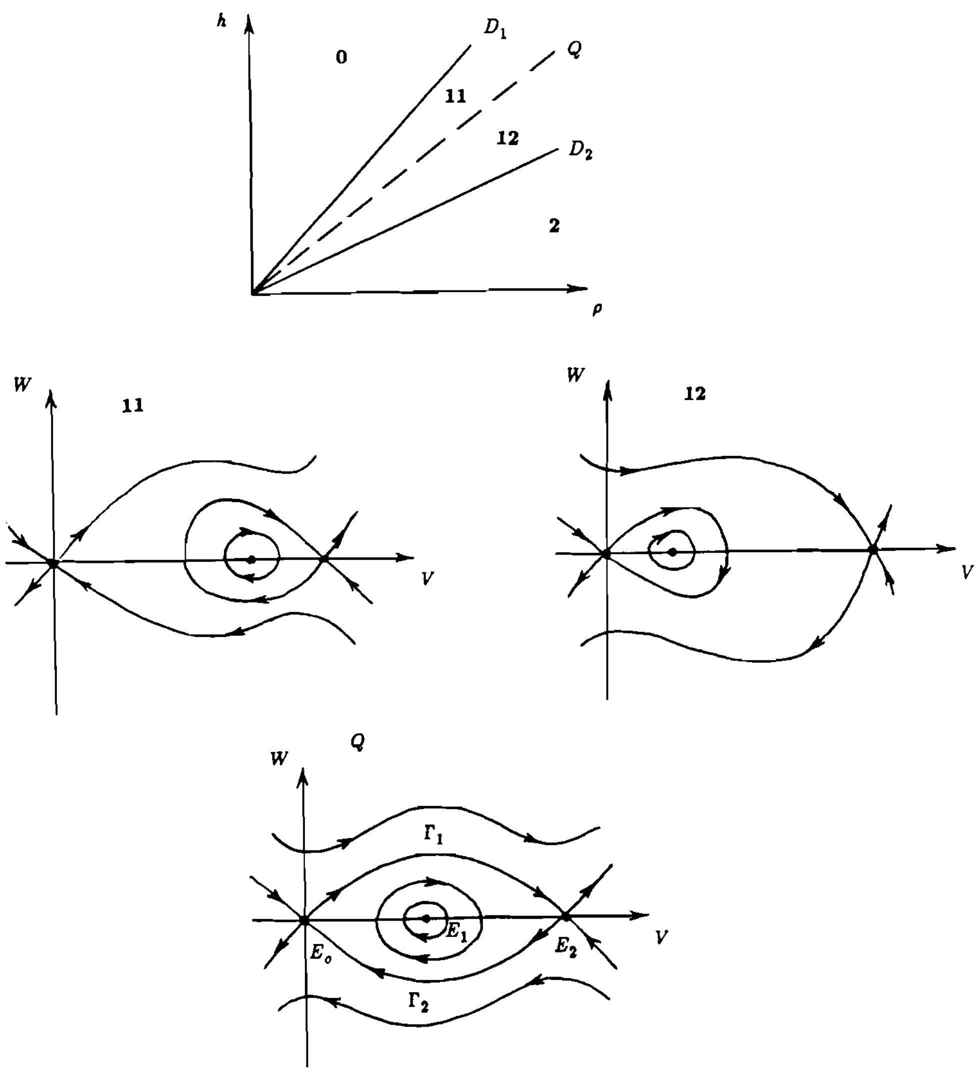

Figure 2: The parameteric and phase portraits of system (6).

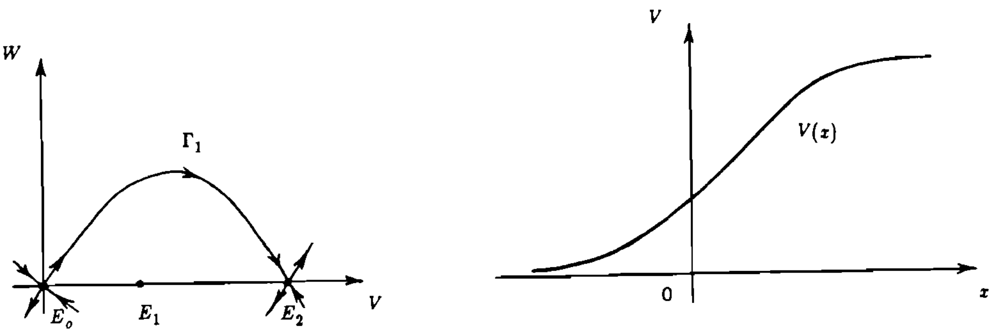

Figure 3: The separatrix connecting saddles corresponds to a standing front in model (4).

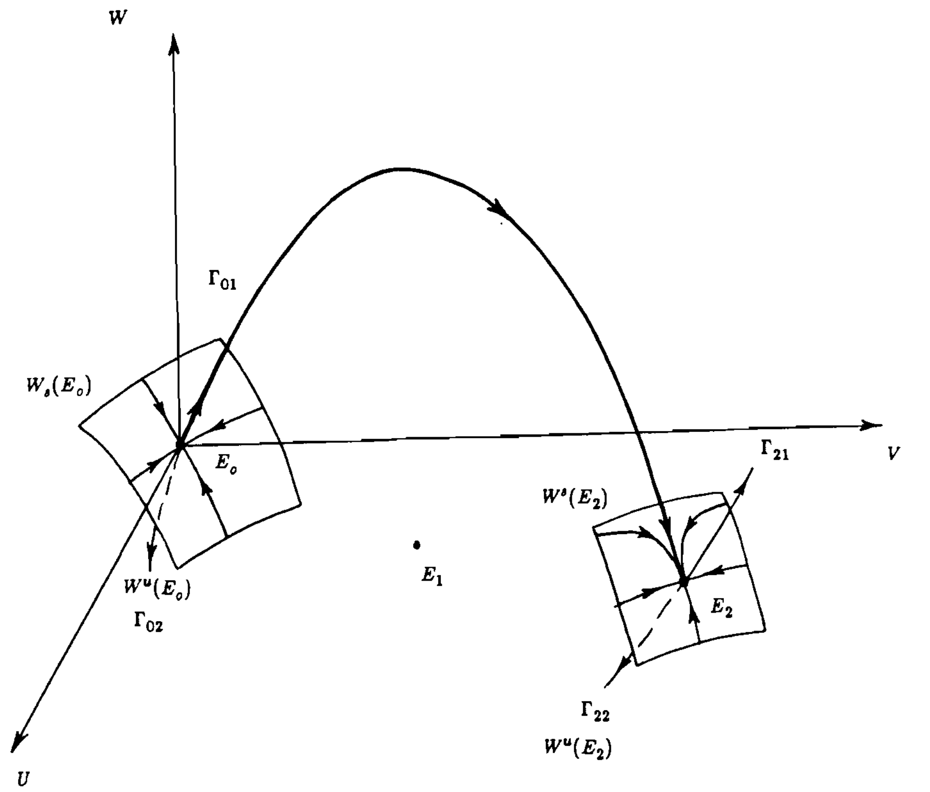

Figure 4: Key elements of the phase portrait of system (8).

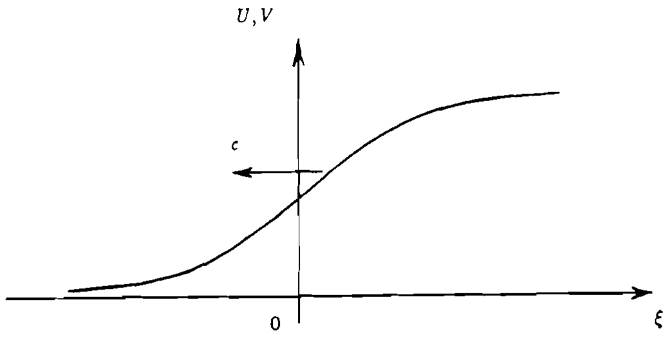

Figure 5: The traveling front in model (4).

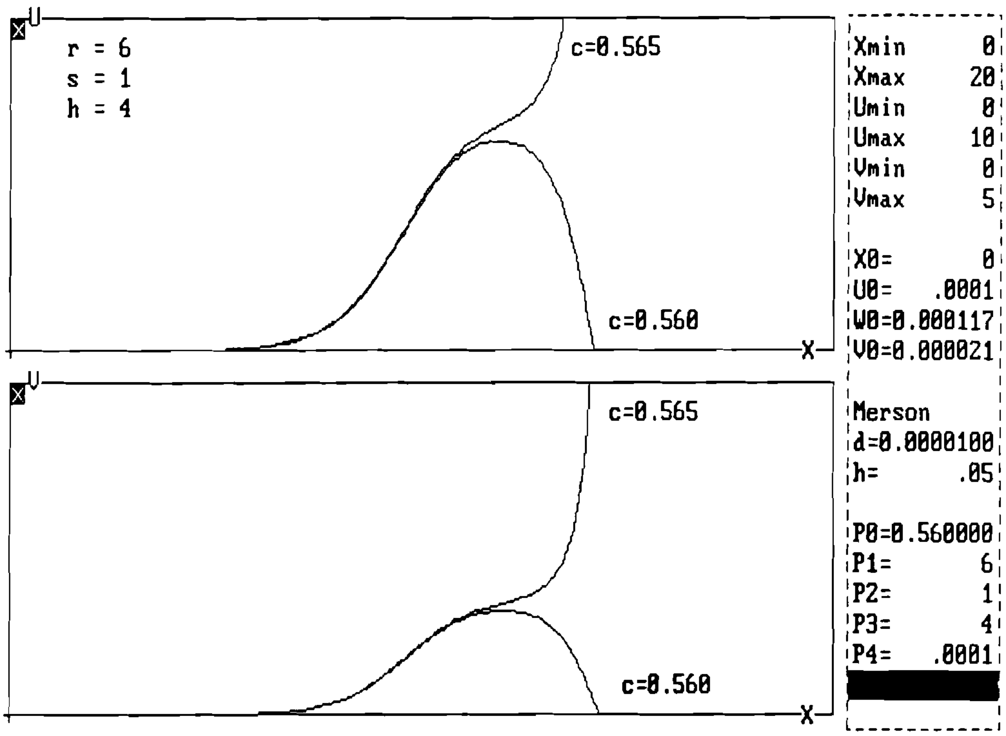

Figure 6: The separatrix behavior for two different parameter c values.

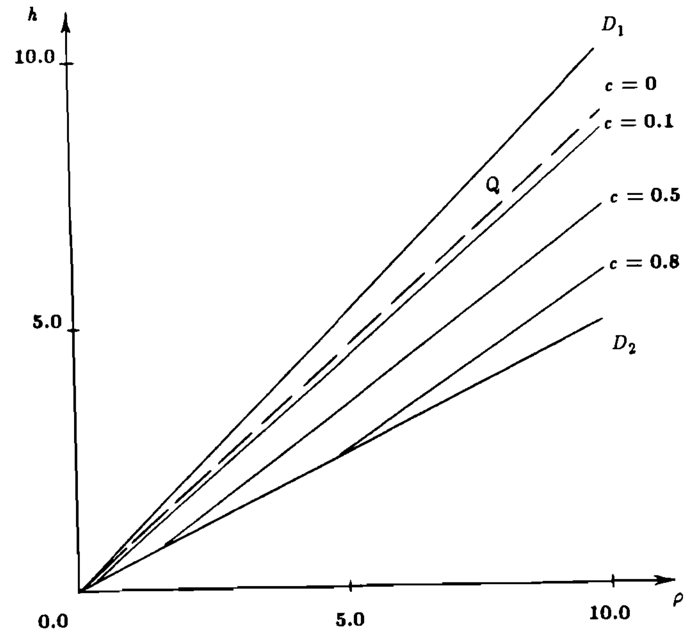

Figure 7: Front constant propagation speed isolines for model (4).