Working Paper

Acid Rain and the Fate of Forest Ecosystems

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WP-94-78
August 1994

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Abstract

In this paper a sixth-order nonlinear dynamical system modelling forest-pests interactions is presented. Forest growth is described by mechanisms of the exchange of carbon and nitrogen between soil and vegetation, and by microbial mineralization. The influence of acid deposition, an increase of which can cause either the decline or the collapse of the forest ecosystem, is discussed. The analysis is carried out by numerically finding the bifurcations of the model.

ACID RAIN AND THE FATE OF FOREST ECOSYSTEMS

Alessandra Gragnani and Sergio Rinaldi

1. INTRODUCTION

Acid depositions have caused, during recent decades, great damages to forests or, more generally, to forest ecosystems. In fact, the increase in acidity causes accumulation of stress in the forest with different consequences. As a first possibility, the forest may smoothly decline: the vegetation biomass decreases slowly, say at the same speed at which acidity increases. On the contrary, the second possible consequence is a collapse: the forest, having reached a suitable threshold of stress, quickly becomes infested and its biomass decreases substantially. The first case corresponds to a non-catastrophic bifurcation of the system, while the second to a catastrophic bifurcation (Guckenheimer and Holmes, 1983).

This paper's aim is to determine under which circumstances the increase in acid deposition, i.e., the decrease in pH of the rain, will generate a decline or a collapse in a given forest. Until now, many results have been obtained by studying the influence of acid deposition on forests (Gatto and Rinaldi, 1987, 1989; Lohele, 1989; Gatto et al., 1993) or, more generally, on forest ecosystems (Muratori and Rinaldi, 1989). However, all of these studies are based on naive models of the vegetation growth, such as the logistic equation

$$\dot{v}(t) = r\, v(t) \left(1 - \frac{v(t)}{\overline{v}}\right)$$

where v(t) is vegetation biomass at time t and r and $\overline{v}$ are intrinsic growth rate and carrying capacity.

In this paper a more realistic model composed by five differential equations that account for the cycles of the mineral nutrients necessary for the growth of the forest biomass, is proposed for describing the vegetation. Therefore, a relatively detailed model based on the description of the exchanges of carbon and nitrogen between soil and vegetation and on microbial mineralization is considered. The rest of the forest ecosystem is composed of defoliator insects or pests feeding only on vegetation, and birds feeding on them; in the following they will be called predators and superpredators, respectively. The model of the forest ecosystem here proposed is, therefore, a three-level food chain composed of prey (vegetation), predator (insect pest), and superpredator (birds). Moreover, it is supposed that the superpredator population is constant since in the majority of the cases birds can feed on alternative resources. The forest ecosystem is, therefore, described by a sixth-order nonlinear dynamical system: five equations describe the vegetation submodel, while the sixth equation describes the dynamic behavior of the predator.

It is practically impossible to detect all modes of behavior of a so complex model, if the parameters are not fixed or constrained to vary in suitable ranges. For this reason, in the following, all parameters are fixed (those of the vegetation submodel correspond to a typical forest of *Pinus Sylvestris*) with the exception of three of them, one for each compartment of the food chain. The three parameters with respect to which the analysis is performed are the acidity of the rain, the maximum uptake rate of the predator and the density of the superpredator. The second of these parameters is, nevertheless, constrained in such a way that the model cannot cycle. This means that the present analysis does not pretend to mimic those forest ecosystems which systematically undergo through recurrent (periodic or almost periodic) infestation episodes.

The paper is organized as follows: in Section 2 the model is described, and in Section 3 all its possible modes of behavior are classified through bifurcations analysis. The catastrophic transitions and the hysteresis emerging from this analysis are discussed in Section 4. Finally, the discussion of the results and possible refinements of the proposed model are presented.

2. THE MODEL

The dynamic of vegetation, in the absence of predators, is described by the exchanges of carbon and nitrogen between vegetation and soil and by microbial mineralization. Our model is based on a series of contributions by Ågren and Bosatta (Ågren and Bosatta, 1987; Ågren, 1988; Bosatta and Ågren, 1991) that the reader can consult for more details. The following phenomena are considered:

- nitrogen is the limiting nutrient for the production of vegetation biomass, while shading reduces the photosynthesis;
- the vegetation absorbs inorganic nitrogen from soil;
- microbial decomposers, whose activity is limited by the amount of carbon in the soil, mineralize organic carbon and nitrogen;
- microbial decomposers immobilize carbon and nitrogen;
- meteorological precipitations enrich the compartment of inorganic nitrogen;
- leaching and washout generate the outflow of inorganic nitrogen and of organic carbon and nitrogen, respectively;
- dead vegetation biomass enriches the compartment of organic carbon and nitrogen.

The following phenomena are considered to describe (see Muratori and Rinaldi, 1989) the dynamic of predators:

- baseline mortality;
- surplus of mortality due to intraspecific competition among predators;
- mortality caused by superpredators.

Lastly, the assumption has been made that predators attack the foliage of the trees: organic nitrogen, mainly contained in leafs, is, therefore, their limiting nutrient.

Under these assumptions, the model is described by the following differential equations with constant parameters

$$\dot{C}_{ov} = (a - bC_{ov})N_{ov} - mC_{ov} \qquad (1a)$$

$$\dot{C}_{OS} = mC_{OV} - u\left(\frac{1}{e} - 1\right)C_{OS} - w_C C_{OS} \tag{1b}$$

$$\dot{N}_{OS} = rmC_{OV} + fuC_{OS} - \frac{u}{e}N_{OS} - w_N N_{OS} \tag{1c}$$

$$\dot{N}_{IS} = \frac{u}{e}N_{OS} - fuC_{OS} + d - lN_{IS} - g\frac{C_{OV}}{q + C_{OV}}\frac{N_{IS}}{h + N_{IS}} \tag{1d}$$

$$\dot{N}_{OV} = -rmC_{OV} + g\frac{C_{OV}}{q + C_{OV}}\frac{N_{IS}}{h + N_{IS}} - \frac{\alpha N_{OV}}{\beta + N_{OV}}P \tag{1e}$$

$$\dot{P} = P\left(\varepsilon\frac{\alpha N_{OV}}{\beta + N_{OV}} - \delta - \gamma P - \frac{\mu S}{\rho + P}\right) \tag{1f}$$

where the variables are:

C_{OV} = organic carbon contained in the vegetation (indicator of the vegetation biomass),

C_{OS} = organic carbon contained in the soil,

N_{OS} = organic nitrogen contained in the soil,

N_{IS} = inorganic nitrogen contained in the soil,

N_{OV} = organic nitrogen contained in the vegetation,

P = density or biomass of predators;

while the parameters have the following meaning:

a = production rate of vegetation biomass (measured in carbon) per unit of nitrogen contained in the vegetation, considered as limiting nutrient;

b = shading rate; bC_{OV} reduces the production rate of the vegetation biomass because of the reduced photosynthesis;

m = mortality rate of vegetation;

u = production rate of microbial biomass per unit of carbon (considered as limiting nutrient for microbes); uC_{os} is the amount of carbon immobilized in the microbial biomass;

e = efficiency of microbial production; uC_{os}/e is the amount of carbon absorbed by decomposers, while its difference with immobilized carbon yields the mineralized carbon;

r = ratio nitrogen/carbon in dead vegetation biomass; rdC_{ov} is the flux of organic nitrogen arising from the death of the vegetation;

f = ratio nitrogen/carbon in the microbial biomass; fuC_{os} is the amount of nitrogen immobilized in the microbial biomass, while uN_{IS}/e is the amount of nitrogen absorbed by microbial decomposers;

w_C, w_N = washout rate for organic carbon and nitrogen;

d = flux of inorganic nitrogen due to precipitation which contains the ions NO_3^- and NH_4^+;

l = rate of leaching;

g = maximum flux of inorganic nitrogen that vegetation can absorb;

h = half saturation constant of the Michaelis-Menten relationship characterizing the absorption of inorganic nitrogen by vegetation;

q = half saturation constant of the Michaelis-Menten relationship characterizing the maximum absorption of inorganic nitrogen by vegetation. In fact, we have assumed that high values of vegetation biomass (expressed by C_{ov}) decrease the absorption of nitrogen per unit of biomass;

α = maximum uptake rate of predators;

β = half saturation constant of the Holling type II functional response (Holling, 1965) of predators, namely the amount of organic nitrogen contained in the vegetation at which the uptake rate is half the maximum;

ε = efficiency of predators;

δ = baseline death rate per capita of predators, namely the death rate at low predators density and in the absence of superpredators;

γ = surplus of death rate due to intraspecific competition among predators;

μ = maximum uptake rate of superpredators;

ρ = half saturation constant of the Holling type II functional response (Holling, 1965) of superpredators, namely the density or biomass of predators at which the uptake rate is half the maximum;

S = density or biomass of superpredators.

The influence of acid deposition is not described in model (1). Denoting with W the flux of protons due to acid deposition (inversely related to rain pH), it has been supposed that:

- the concentration Z of protons in the soil (inversely related to soil pH) is an increasing function of W, in particular,

  $$Z = Z_0\left(1 + q_Z \frac{W - W_0}{W_0}\right) \tag{2}$$

  where Z_0 and W_0 are suitable reference values, as specified in the following, while q_Z is the ratio between the percent variation of Z and that of W with respect to their reference values;
- the flux d of inorganic nitrogen due to precipitation is an increasing function of W, in particular,

  $$d = d_0\left(1 + q_d \frac{W - W_0}{W_0}\right) \tag{3}$$

  where d_0 and W_0 are suitable reference values, as specified in the following, while q_d is the ratio between the percent variation of d and that of W with respect to their reference values;
- the production rate a and the mortality rate m of the vegetation biomass are, respectively, decreasing and increasing function of W (damage of foliage);
- the production rate u of microbial biomass is a decreasing function of Z (influence of soil pH on microbial activity);

- the maximum flux g of inorganic nitrogen that vegetation can absorb is a decreasing function of Z (damage of roots);
- the searching time β of the predators is a decreasing function of W, in particular,

$$\beta = \beta_0 \frac{W_c^4}{W^4 + W_c^4}$$

where β_0 is the maximum searching time, while W_c is the value of W where the searching time β is half the maximum; predators are, therefore, very sensitive to variations in acid depositions just in the vicinity of W_C. This can be justified by considering the effects of acid depositions on vegetation. There can be, for example, foliar damage resulting in erosion of the leaf cuticle whose integrity is a mechanism of resistance against predators. The increase in acid deposition increases the density of points at which the resource can be successfully attacked by predators so that their searching time decreases.

Table 1 summarizes the ranges of variability of the parameters of model (1) and their functional dependence upon the exogenous parameter W. The values are typical for forests of *Pinus Sylvestris* (Ågren and Bosatta, 1987; Ågren, 1988; Ingestad and Ågren, 1991; Bosatta and Ågren, 1991). Reference values and ranges of variability for the parameters of the predators are not given, since they are only roughly known.

3. BIFURCATION ANALYSIS OF THE MODEL

In this Section all modes of behavior of model (1) corresponding to different values of W (flux of protons), S (density of superpredator), and α (maximum uptake rate of predator) are detected. This is done through a systematic bifurcation analysis of the equilibria which is performed numerically by fixing all other parameters at reference values.

With regard to the equilibria, there may exist two trivial equilibria; the first corresponds to absence of vegetation (and predators), namely to the presence of inorganic nitrogen in the soil only ($\overline{N}_{IS}$ = d/l), while the second corresponds to forest at its "carrying capacity". This last equilibrium, denoted by $(\overline{V},0)$, where the vector

$$\overline{V} = (\overline{C}_{OV}, \overline{C}_{OS}, \overline{N}_{OS}, \overline{N}_{IS}, \overline{N}_{OV})$$

represents the equilibrium values of the five variables characterizing the vegetation submodel, corresponds to a healthy (i.e. not infested) forest. Moreover, there may exist strictly positive equilibria corresponding to forests infested by pests.

The trivial equilibrium $(\overline{V},0)$ (healthy forest) exists for sufficiently high acidity of the rain (W) and is unique as prooved in the Appendix where it is also shown that the equilibrium $\overline{V}$ in the state space V of the vegetation submodel with P = 0 is asymptotically stable. However, for suitable values of W, S and α the equilibrium $(\overline{V},0)$ can become unstable in the whole space (V,P) of the system, formally via transcritical bifurcation. In other words, for suitable values of the free parameters the predators can invade the healthy forest.

The relationship among parameters characterizing this bifurcation (as well as those presented in the following) cannot be found analytically because of the complexity of the model. Nevertheless, by means of LOCBIF, a program implementing a powerful continuation technique for bifurcation analysis (Khibnik et al., 1993), it has been possible to numerically detect all bifurcations characterizing system (1) and to display them in any two-dimesional parameter space. In the following the bifurcation curves are shown in the parameter space (W,S) because the flux W of protons due to acid deposition is the most interesting exogenous variable, while the density S of superpredators can be considered to a certain extent a control variable. The analysis will show that at different levels of S there are different kinds of impacts of acid depositions on forests, and that the bifurcation diagram is more complex for more voracious predators (i.e. when α is greater).

The parameters characterizing predators and superpredators (with the exception of the maximum uptake rate of predators α) have been fixed at the following values

$\beta_0 = 300$ [kgN ha^{-1}] $W_c = 1$ [keq ha^{-1} y^{-1}] $\delta = 0.5$ [y^{-1}]

$\gamma = 0.15$ [kgN^{-1} ha y^{-1}] $\mu = 0.33$ [y^{-1}] $\rho = 0.33$ [kgN ha^{-1}] $\varepsilon = 0.5$

Moreover, it has been assumed that $q_Z = 0$ and $q_d = 1$ in eqs. (2) and (3), i.e., a percent variation on the flux of protons W implies no influence on the soil pH, which is inversely related to Z, and the same variation on the flux d of nutrient.

Figure 1 is the bifurcation diagram in the parameter space (W,S) corresponding to the above parameter setting and to $\alpha = 1.5$. The curve corresponding to eq. (A2) in the Appendix does not appear in this figure because the threshold value of W is smaller than 1 (actually much smaller than 1). In this diagram there are two different bifurcation curves, identified with symbols, namely T for transcritical bifurcation and F for fold bifurcation. These curves define, in the parameter space (W,S), three different regions, indicated by [a], [b], and [c]. For parameter values corresponding to points in region [a], all trajectories tend toward the trivial equilibrium $(\overline{V},0)$ (healthy forest), as shown in fig. 2a, while in region [c] all trajectories tend toward the equilibrium corresponding to forest infested by predators, as shown in fig 2c. In region [b] there are two stable equilibria (namely the healthy forest $(\overline{V},0)$ and the infested forest), whose basins of attraction are limited by the inset of a saddle-type equilibrium. Depending upon the initial conditions, the system tends toward one of the two stable equilibria, as shown in fig. 2b.

Crossing the fold bifurcation curve F from region [b] to region [a], the stable equilibrium corresponding to the infested forest and a saddle collide and disappear. Crossing the transcritical bifurcation curve T from region [a] to region [c], the trivial equilibrium $(\overline{V},0)$ looses stability and the healthy forest gradually becomes infested, while, crossing curve T from region [b] to region [c] the trivial equilibrium $(\overline{V},0)$ corresponding to the healthy forest collides with the saddle and becomes unstable.

Increasing the maximum uptake rate of the predator (α) the bifurcation diagram becomes reacher. Fig. 3 shows, for example, the bifurcation curves obtained for $\alpha = 3.9$. As before, there is one region (grey region) with two stable equilibria but the bifurcation curves are four, namely F, T, H, and M for fold, transcritical, Hopf, and homoclinic bifurcation, respectively. The first three of these curves have been computed with LOCBIF while the last one, namely M has been computed only at a few points with a special program. These curves define, in the parameter space (W,S) five different regions, indicated by [a'], [a''], [b'], [b''], and [c]. The asymptotic behavior of model (1) in regions [a]=[a']$\cup$[a"], [b]=[b']$\cup$[b"], and [c] of fig. 3 is the same as in regions [a], [b], and [c] of fig. 1, respectively. In region [a"], there are two non trivial saddle-type equilibria; crossing the fold bifurcation curve F from this region to region [a'], they collide and disappear. In region [b"] there is a saddle equilibrium and a saddle-cycle obtained through subcritical Hopf bifurcation H; crossing this curve from region [a"] to region [b"], the saddle equilibrium becomes stable and a saddle-cycle appears. Such a cycle disappears through homoclinic bifurcation crossing curve M from region [b"] to region [b']. The point BT from which the three curves F, H, and M originate is a Bogdanov-Takens codimension-2 bifurcation point (see Guckenheimer and Holmes, 1983).

The analysis of figs. 1 and 3 shows that, looking only at the attractors (i.e. at the stable equilibria) of model (1), the parameter space (W,S) is partitioned into three regions, corresponding to three different asymptotic modes of behavior of the system. In region [a], characterized by high values of rain pH (i.e., low values of W), the forest tends toward its carrying capacity and the predators are absent. In the second region ([b]), characterized by intermediate values of rain pH, the forest can be either healthy or infested and accidents like fires and diseases can bring the system from one basin of attraction to the other. Finally, in the last region ([c]), characterized by low values of pH, the forest can only be infested.

4. CATASTROPHES AND HYSTERESES

A more detailed analysis of the bifurcation diagrams of figs. 1 and 3 suggests other conclusions. First of all, the variation in rain acidity, i.e., in W, with a constant superpredator population S, can generate catastrophic transitions from a healthy to an infested forest as well as vice versa. For example, if the system is in region [b] close to curve T (see figs. 1 and 3) and the forest is healthy, a small decrease of rain pH that implies the crossing of curve T would give rise to a catastrophic transition ending with an infested forest. This dramatic transition of the forest ecosystem may last a long time, even years. Fig. 4 shows one of these transients obtained through simulation by linearly increasing over time the flux of protons W in the neighborhood of its catastrophic value (the parameter values are those of fig. 3). The duration of the transient is of about 20 years, but small damped oscillations, typical of predator-prey systems, are present for a longer time.

Catastrophic transitions are also obtained by increasing rain pH provided the left boundary of the grey region of figs. 1 and 3 is crossed from [b] to [a]. In this case, the catastrophe will actually be a regeneration of the vegetation biomass.

The existence of catastrophic transitions, either increasing or decreasing the acid deposition, gives rise to a "hysteresis" between the two equilibria corresponding to healthy and infested forest. Fig. 5 shows this hysteresis in terms of vegetation density (the parameters are those of fig. 1). The upper solid line corresponds to forest at its carrying capacity, while the lower to infested forest; a slow periodical variation of rain pH encompassing the two critical values of W would, therefore, result in an hysteretic cycle between the two equilibria.

It is important to remark that the transition from healthy to infested forest and the reverse one from infested to healthy forest can also take place gradually. This happens when the dashed part of the transcritical bifurcation curve T of figs. 1 and 3 is crossed. The bifurcation diagrams show that this should be expected in forest with low density of superpredators. The biological interpretation of this result is the following. The presence of a great number of insectivores can keep the pest under control even when a quite low rain pH favours the growth of insect pest. But above a threshold value, because of the limited harvesting capacity of the superpredator, each extra unit of pest is fully uncontrolled and can therefore give rise to a demographic explosion (catastrophe). On the contrary, if birds are not too many, and acidity increases slowly, than the pest can gradually take advantage of the increasing damages in the foliage and smoothly increase its density.

5. CONCLUDING REMARKS

In this paper the impact of acid deposition on forest ecosystems has been investigated by means of a mathematical model (eq. (1)) in which the vegetation growth is described by the exchanges of carbon and nitrogen with soil. The analysis of the bifurcations of the equilibria of this model has allowed the classification of the nature of the impact: a smooth decline or a dramatic collapse from a healthy to an infested forest may arise, when acid deposition increases too much. The bifurcation diagrams (see figs. 1 and 3) show that a possible way to temporarily avoid damages on the forest is to compensate the increase of acidity by stocking superpredators. However, in doing so, there are higher chances that the forest will soon or late suffer a catastrophic collapse. The bifurcation diagrams also show that drops in the birds population controlling the pest can also induce catastrophic transitions from healthy to infested forest and that this is more likely to occur if the rain pH is low.

The results of the analysis presented in this paper are in agreement with those obtained by Muratori and Rinaldi (1989) with a simpler model (logistic equation for the vegetation growth). Their analysis shows an extra mode of behavior, namely the case in which the forest is periodically infested by pests. This case is missing in the present analysis because it has been intentionally left out by limiting the range of variation of the maximum uptake rate of the insect pest. Indeed, it can be easily checked, for example, by simulation, that, increasing such a parameter, also the model proposed in this paper gives rise to stable limit cycles, which somehow mimic the behavior of periodically infested forests. Actually, a preliminary analysis has shown that there is evidence of period doubling bifurcations of these limit cycles which might indicate the presence of deterministic chaos in suitable niches of the parameter space. This suggests that the behavior of model (1), because of the detailed description for the vegetation growth, is significantly reacher than the second-order model used in Muratori and Rinaldi (1989); and possibly of the same complexity of food chain models which have recently been proved to be chaotic (Hastings and Powell, 1991; Rai and Sreenivasan, 1993; Abrams and Roth,1994a, b; Klebanoff and Hastings, 1994; McCann and Yodzis, 1994a, b). Forgetting the problem of the impact of acid precipitation, model (1) seems therefore a good candidate for studying the randomness of the recurrent infestation episodes of some forests.

REFERENCES

Abrams, P. A. and Roth, J. D. (1994a). The responses of unstable food chains to enrichment. *Evolutionary Ecology*, **8**, 150-171.

Abrams, P. A. and Roth, J. D. (1994b). The effects of enrichment of three-species food chains with nonlinear functional responses, *Ecology*, **75**, 1180-1130.

Ågren, G. I. (1988). Ideal nutrient productivities and nutrient proportions in plant growth, *Plant, Cell and Environment*, **11**, 613-620.

Ågren, G. I. and Bosatta, E. (1987). Theoretical analysis of the long-term dynamics of carbon an nitrogen in soil, *Ecology*, **68**(5), 1181-1189.

Bosatta, E. and Ågren, G. I. (1991). Dynamics of carbon and nitrogen in the organic matter of the soil: a generic theory, *The American Naturalist*, **138**(1), 227-245.

De Leo, G., Del Furia, L., and Gatto, M. (1993). The interaction between soil acidity and forest dynamics: a simple model exhibiting catastrophic behavior, *Theoretical Population Biology*, **43**(1), 31-51.

Gatto, M. and Rinaldi, S. (1987). Some models of catastrophic behavior in exploited forests, *Vegetatio*, **69**, 213-222.

Gatto, M. and Rinaldi, S. (1989). Acid deposition and catastrophes in forests: A tree nutrient model, *Coenoses*, **4**, 81-90.

Guckenheimer, J. and Holmes, P. (1983). *Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields*, Springer Verlag, New York, Heidelberg, Berlin, Tokyo.

Hastings, A. and Powell, T. (1991). Chaos in a three-species food chain, *Ecology*, **72**(3), 896-903.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, **45**, 5-60.

Ingestad, T. and Ågren, G. I. (1991). The influence of plant nutrition on biomass allocation, *Ecological Applications*, **1**(2), 168-174.

Khibnik, A. I., Kuznetsov, Yu. A., Levitin, V.V., Nikolaev, E. V. (1993). Continuation techniques and interactive software for bifurcation analysis of ODEs and iterated maps, *Physica D*, **62**, 360-370.

Klebanoff, A and Hastings, A (1994). Chaos in a Three species food chain. *Journal of Mathematical Biology*, **32**, 427-451.

Lohele, C. (1989). Forest-level analysis of stability under exploitation: depensation responses and catastrophe theory, *Vegetatio*, **79**, 109-115.

Muratori, S. and Rinaldi, S. (1989). Catastrophic bifurcations in a second-order dynamical system with application to acid rain and forest collapse, *Applied Mathematical Modelling*, **13**, 674-681.

McCann, K. and Yodzis, P. (1994a). Biological conditions for chaos in a three-species food chain. *Ecology*, **75**, 561-564.

McCann, K. and Yodzis, P. (1994b). Bifurcation structure of a three-species food chain. *Theoretical Population Biology*, (to appear).

Rai, V. and Sreenivasan, R. (1993). Period-doubling bifurcations leading to chaos in a model food chain. *Ecological Modelling*, **69**, 63-77.

APPENDIX

This Appendix is devoted to the proof of the uniqueness and stability of the vector $\overline{V}$.

By annihilating the right-hand sides of (1a)-(1e) with $P = 0$ and $\overline{C}_{\mathrm{OV}} \neq 0$, and rearranging the equations one obtains

$$\overline{C}_{\mathrm{OV}} = \frac{g}{rm}\frac{\overline{N}_{\mathrm{IS}}}{h+\overline{N}_{\mathrm{IS}}} - q$$

$$\overline{N}_{\mathrm{OV}} = \frac{m\overline{C}_{\mathrm{OV}}}{a - b\overline{C}_{\mathrm{OV}}}$$

$$\overline{C}_{\mathrm{OS}} = \frac{m\overline{C}_{\mathrm{OV}}}{w_C + u\left(\frac{1}{e} - 1\right)}$$

$$\overline{N}_{\mathrm{OS}} = \frac{rm\overline{C}_{\mathrm{OV}} + fu\overline{C}_{\mathrm{OS}}}{w_N + \frac{u}{e}}$$

$$\frac{w_N}{w_N + \frac{u}{e}}\left(r + \frac{fu}{w_C + u\left(\frac{1}{e} - 1\right)}\right)\left(\frac{g}{r}\frac{\overline{N}_{\mathrm{IS}}}{h+\overline{N}_{\mathrm{IS}}} - qm\right) = d - l\overline{N}_{\mathrm{IS}} \qquad \text{(A1)}$$

Solving eq. (A1) with respect to $\overline{N}_{IS}$, all the other variables are univocally determined. On the other hand, the solution $\overline{N}_{IS}$ of eq. (A1) is unique since the left and the right-hand sides of the equation are respectively increasing and decreasing with $\overline{N}_{IS}$.

If $\overline{C}_{OV}$ is equal to 0, in the absence of predators (P = 0), i.e. if

$$\frac{g}{rm}\frac{\overline{N}_{IS}}{h+\overline{N}_{IS}}=q$$

one obtains $\overline{C}_{OS} = \overline{N}_{OV} = \overline{N}_{OS} = 0$, and $\overline{N}_{IS} = d/l$. In other words, the two trivial equilibria, corresponding to absence of vegetation and to forest at its carrying capacity, collide for

$$\frac{g}{rm}\frac{d}{hl+d}=q \qquad \text{(A2)}$$

Eq. (A2), taking into account eqs. (2) and (3) and the dependence of g and d upon Z and W (see table 1) can be solved with respect to W, thus giving a threshold for W, below which vegetation cannot exist. On the contrary, for W above the threshold, the equilibrium ($\overline{V}$,0) exists, and is stable in the state space V characterizing the vegetation model. A formal proof of the stability of $\overline{V}$ could be as follows. First evaluate the Jacobian matrix J of eqs. (1a)-(1e) with P = 0 at $\overline{V}$

$$J=\begin{bmatrix} -m-b\overline{N}_{OV} & 0 & 0 & 0 & a-b\overline{C}_{OV} \\ m & -u\left(\frac{1}{e}-1\right)-w_C & 0 & 0 & 0 \\ rm & fu & -\frac{u}{e}-w_N & 0 & 0 \\ -g\frac{q}{\left(q+\overline{C}_{OV}\right)^2}\frac{\overline{N}_{IS}}{h+\overline{N}_{IS}} & -fu & \frac{u}{e} & -l-g\frac{\overline{C}_{OV}}{q+\overline{C}_{OV}}\frac{h}{\left(h+\overline{N}_{IS}\right)^2} & 0 \\ -rm+g\frac{q}{\left(q+\overline{C}_{OV}\right)^2}\frac{\overline{N}_{IS}}{h+\overline{N}_{IS}} & 0 & 0 & g\frac{\overline{C}_{OV}}{q+\overline{C}_{OV}}\frac{h}{\left(h+\overline{N}_{IS}\right)^2} & 0 \end{bmatrix}$$

Then compute the five eigenvalues $\lambda_1,\ldots,\lambda_5$ of such a matrix and check that they have negative real part. This procedure applied for the reference parameter setting gives

$$J = \begin{bmatrix} -0.9796 & 0 & 0 & 0 & 2.8164 \\ 0.3750 & -0.6843 & 0 & 0 & 0 \\ 0.0037 & 0.0112 & -0.9647 & 0 & 0 \\ -0.0004 & -0.0112 & 0.9347 & -0.3086 & 0 \\ -0.0033 & 0 & 0 & 0.0086 & 0 \end{bmatrix}$$

and

$\lambda_1 = -0.97+i\,0.02 \qquad \lambda_2 = -0.97-i\,0.02 \qquad \lambda_3 = -0.68 \qquad \lambda_4 = -0.31 \qquad \lambda_5 = -0.94 \cdot 10^{-2}$

so that one can conclude that the equilibrium $\overline{V}$ is indeed asymptotically stable. One could actually do more than this by proving the stability of such an equilibrium for any parameter setting but the proof is omitted since it requires the use of specialized software for algebraic manipulations. On the other hand, the stability of $\overline{V}$, once we have found that $\overline{V}$ is unique, is obvious from a biological point of view.

Therefore, because of its uniqueness and stability in the state space V, the vector $\overline{V}$ can be identified with the carrying capacity of the forest.

TABLE 1

Dimensions, ranges of variability, and reference values of the parameters characterizing the vegetation submodel. Reference is made to a forest of *Pinus Sylvestris*. Z and d depend upon W by eqs. (2) and (3).

Parameter		Dimension	Min	Max	Reference value
W		keq ha^{-1} y^{-1}	0	10	2
Z		eq l^{-1}	10^{-5}	10^{-3}	10^{-4}
d		kgN ha^{-1} y^{-1}	1	100	10
$a = a_0 \exp(-k_a W)$	a_0	kgC kgN^{-1} y^{-1}	10	30	20
	k_a	keq^{-1} ha y			0.5
b		kgN^{-1} ha y^{-1}	0.001	0.003	0.002
$m = m_0/(1-W/W^*)$	m_0	y^{-1}	0.1	0.5	0.3
	W^*	keq ha^{-1} y^{-1}			10
$u = u_0 \frac{1-k_u Z/Z^*}{1-Z/Z^*}$	u_0	y^{-1}	0.1	0.5	0.3
	k_u				3
	Z^*	eq l^{-1}			$10^{-2.5}$
e			0.1	0.5	0.3
r		kgN kgC^{-1}			0.01
f		kgN kgC^{-1}			0.04
l		y^{-1}	0.01	1	0.3
w_C		y^{-1}			0.03
w_N		y^{-1}			0.03
$g = g_0 \exp(-k_g Z^3)$	g_0	kgN y^{-1}	5	20	10
	k_g	eq^{-3} l^3			$5 \cdot 10^9$
q		kgC ha^{-1}	100	1000	300
h		kgN ha^{-1}	0.1	100	1

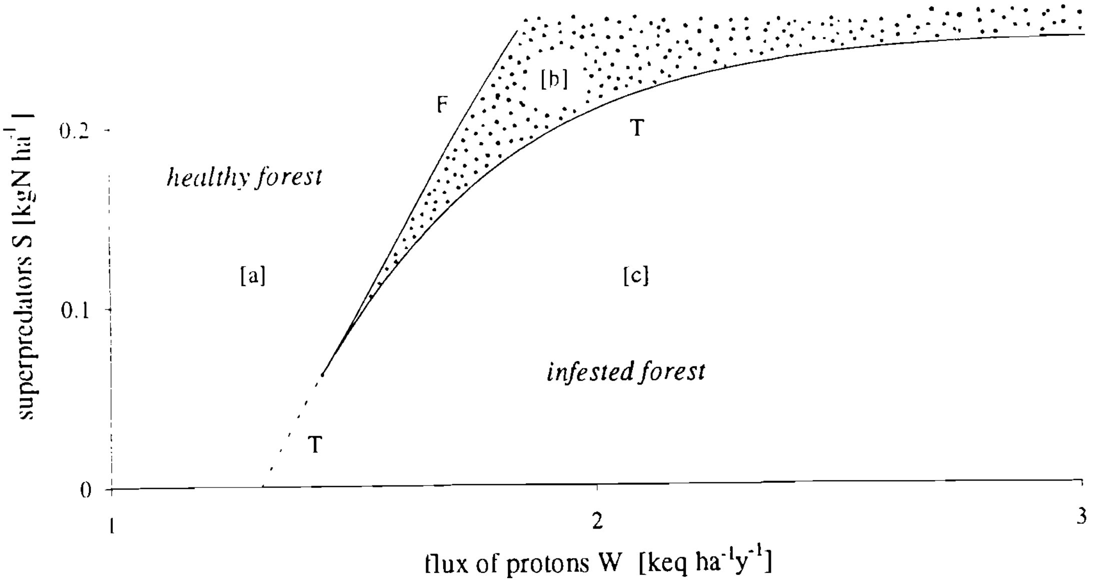
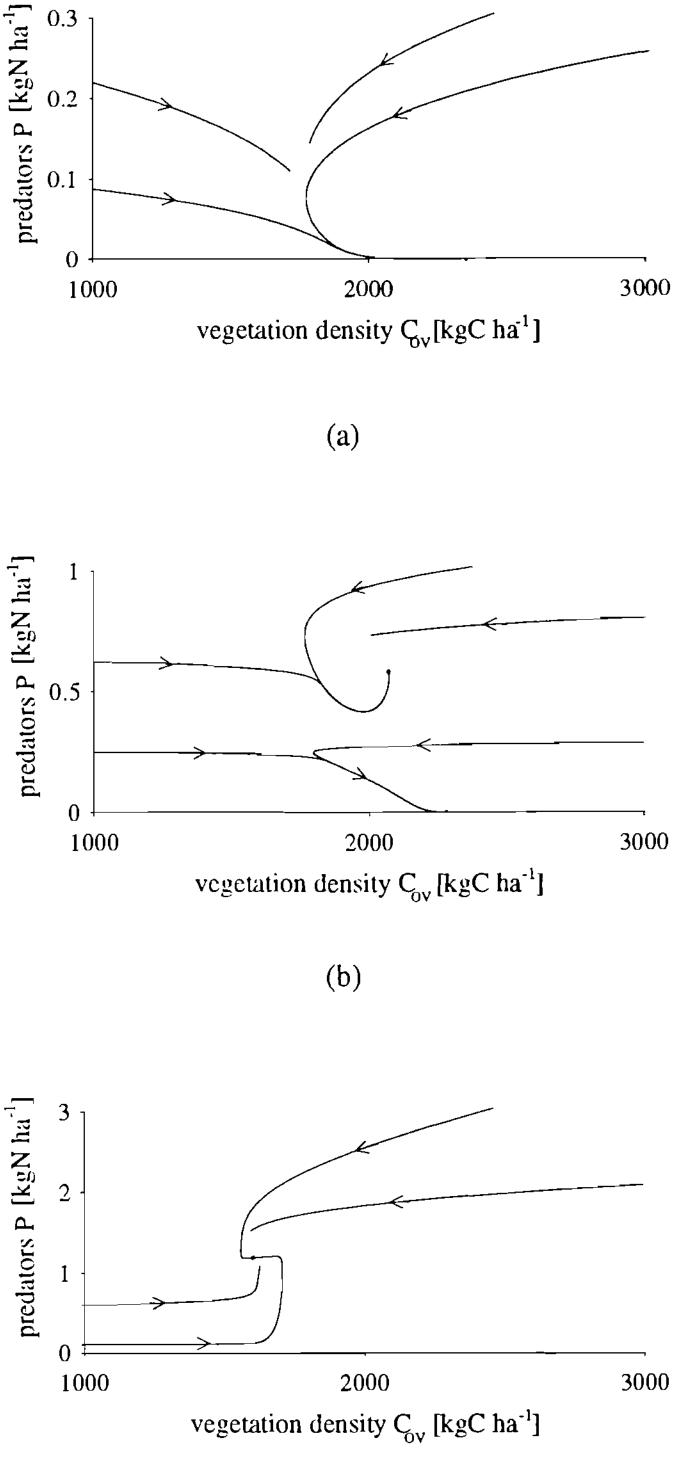


Fig. 1 Bifurcation diagram of system (1) for the reference parameter values and $\alpha = 1.5$. F and T indicate, respectively, fold and transcritical bifurcation curves. In the grey region [b] there are two stable equilibria, namely healthy and infested forest.



(c)

Fig. 2 Projections of state trajectories of system (1) in the state space (C_{0v},P) for the reference parameter values, $\alpha = 1.5$, and $S = 0.23$: (a) $W = 1.5$; (b) $W = 1.85$; (c) $W = 2.5$, corresponding, respectively, to systems in regions [a], [b], and [c] of fig. 1.

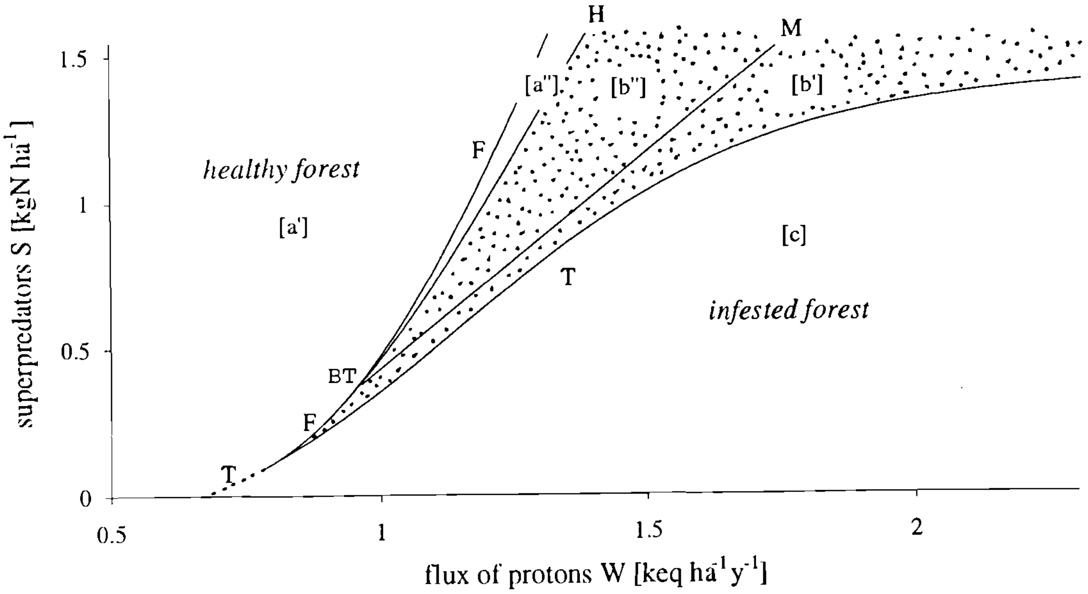


Fig. 3 Bifurcation diagram of system (1) for the reference parameter values and $\alpha = 3.9$. Curves F, T, H, and M indicate, respectively, fold, transcritical, Hopf and homoclinic bifurcations. In the grey region there are two stable equilibria.

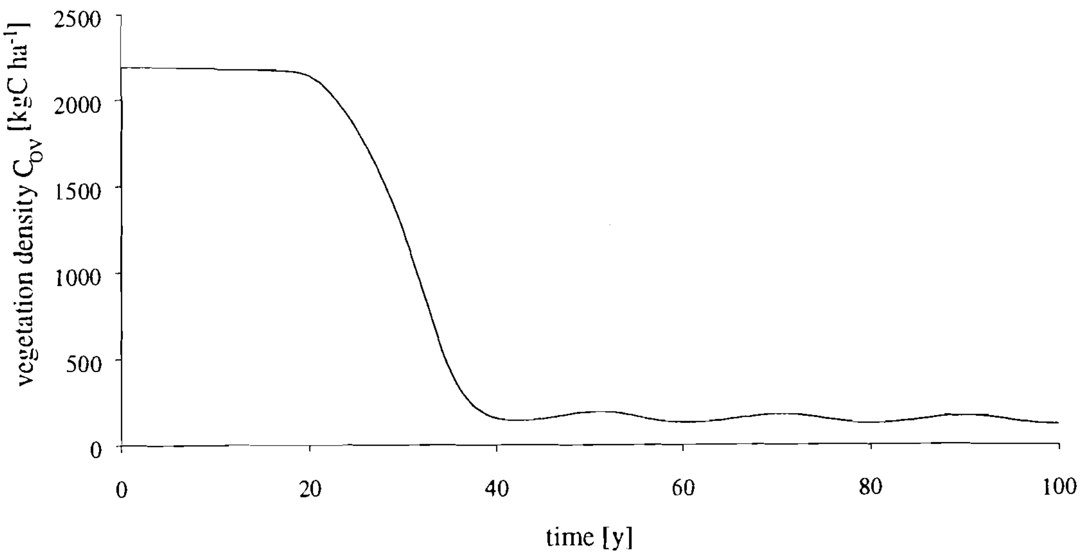


Fig. 4 Simulation of vegetation density (indicated by C_{ov}) for $\alpha = 3.9$, $S = 1.4$, and all other parameters at their reference values. The plot is obtained starting with a forest at its carrying capacity and with a small density of predators ($P = 1.65 \cdot 10^{-2}$) and increasing linearly (5% in 100 years) the flux of protons W from its catastrophic value (readable in fig. 3).

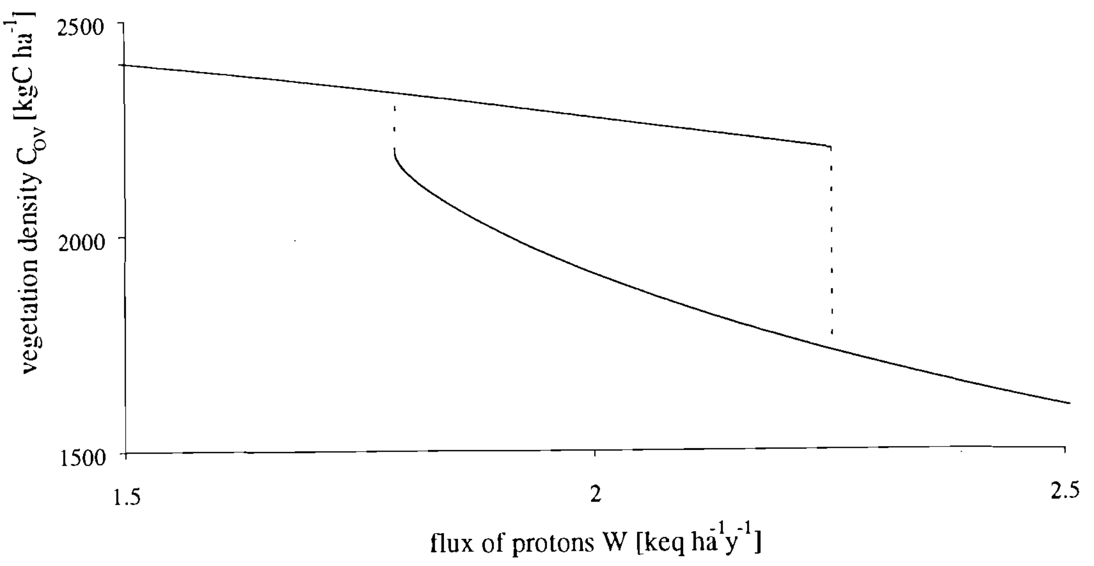


Fig. 5 Hysteresis of vegetation density (indicated by C_{ov}) for $\alpha = 1.5$, $S = 0.23$, and for the reference parameter values. The dashed lines indicate catastrophic transitions; the upper solid line refers to healthy forest, while the lower to infested forest.