

Acidic Deposition, Plant Pests, and the Fate of Forest Ecosystems

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We present and analyze a nonlinear dynamical system modelling forest-pests interactions and the way they are affected by acidic deposition. The model includes mechanisms of carbon and nitrogen exchange between soil and vegetation, biomass decomposition and microbial mineralization, and defoliation by pest grazers, which are partially controlled by avian or mammalian predators. Acidic deposition is assumed to directly damage vegetation, to decrease soil pH, which in turn damages roots and inhibits microbial activity, and to predispose trees to increased pest attack. All the model parameters are set to realistic values except the inflow of protons to soil and the predation mortality inflicted to the pest which are allowed to vary inside reasonable ranges. A numerical bifurcation analysis with respect to these two parameters is carried out. Five functioning modes are uncovered: (i) pest-free equilibrium; (ii) pest persisting at endemic equilibrium; (iii) forest-pest permanent oscillations; (iv) bistable behavior with the system converging either to pest-free equilibrium or endemic pest presence in accordance with initial conditions; (v) bistable behavior with convergence to endemic pest presence or permanent oscillations depending on initial conditions. Catastrophic bifurcations between the different behavior modes are possible, provided the abundance of predators is not too small. Numerical simulation shows that increasing acidic load can lead the forest to collapse in a short time period without important warning signals. © 1998 Academic Press

1. INTRODUCTION

Air pollution poses a serious danger to terrestrial ecosystems. In Europe more than 80% of conifer forests and about 40% of deciduous ones suffer from excessive pollution loading. Forest decline has been recognized in France, Germany, Austria, Switzerland and northern Italy in the 1980s. This has been at least partially ascribed to SO_2 , NO_x , O_3 , acidic deposition and a variety of trace gases (Zöttl and Hüttl, 1986; Rehfuess, 1987). In North America the extent of forest exposure to air pollution appears to be far greater than previously assumed (NADP, 1991), even if clear effects have not been documented yet. Statistical analysis of field data, laboratory experiments and the understanding of plant physiology and soil biochemistry have unraveled a host of different

mechanisms through which acidic precipitation and, more in general, air pollution influence plant survival, growth and reproduction (Krause, 1989). In the past, the scientists' attention was mainly focused on the most direct, conspicuous and dramatic effects associated with power plants, smelters or factories. More recent research developments have evidenced the existence of subtle, cumulative, indirect effects caused by moderate, but chronic exposure. It is now clear that some pollutants act on soil chemistry and ecosystem nutrient cycling (Johnson and Lindberg, 1992) as well as on interspecific plant competition.

The alteration of plant-pest interactions is another indirect effect that is being considered as a causative agent of forest decline. In fact, air pollution can increase the susceptibility of a plant species to the attack of animal pests and pathogens (although it is worthwhile citing that in some cases it could reduce damage by inhibiting

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pests). According to Smith *et al.* (1984), the potential mechanisms are as follows:

— alteration of tree morphology, physiology, metabolism or chemistry by acidic deposition may predispose forest trees to enhanced pathogen or insect activity;

— acidic deposition may directly stimulate or benefit phytophagous insects such that insect stress on host trees is increased;

— acidic deposition may directly stimulate or benefit microbial pathogens such that disease stress on host trees is increased.

Taylor, Johnson, and Andersen (1994) cite altered carbon metabolism as a possible culprit. As defense compounds have lower priority for carbon allocation, the photosynthate available for withstanding pathogens may be insufficient when air pollution poses additional demands on carbon resources. These authors quote the ponderosa pine (*Pinus ponderosa*) trees in the San Bernardino Mountains of southern California as one of the best documented examples. The trees have been exposed to high ozone levels from the Los Angeles basin since the early 1950s (Miller, 1973) with the consequence of foliar injury, premature leaf fall, reduced nutrient retention in the foliage. As a result, the weakened trees have been more susceptible to root rot (*Fomes annosus*) and pine beetles (*Dendroctonus brevicomis*), the dominant pests in this region (Cobb and Stark, 1970).

This paper's aim is to determine under which circumstances the increase in acidic deposition will generate a smooth decline or a collapse in a forest characterized by important interactions with animal pests. Until now, many results have been obtained by studying minimal models that describe the influence of acidic deposition on forest vegetation (Gatto and Rinaldi, 1987, 1989; Lohele, 1989; De Leo *et al.*, 1993) or, more generally, forest ecosystems (Muratori and Rinaldi, 1989). However, all of these studies are based on naive paradigms of vegetation growth, basically one-dimensional models.

In this paper the vegetation dynamics is described by a more realistic model, which accounts for the cycles of mineral nutrients necessary for the growth of the forest biomass. It consists of five differential equations that describe the exchanges of carbon and nitrogen between soil and vegetation while considering the role of microbial mineralization. The rest of the forest ecosystem is composed of pests feeding on vegetation only, and birds or small mammals preying on them; in the following they will be called defoliators and predators, respectively. The proposed model is, therefore, a three-trophic food chain

composed of a bottom level (vegetation), an intermediate one (defoliators), and a top level (predators). However, it is supposed that the dynamics of the predator population can be neglected, since in most cases birds and mammals can feed on resources alternative to the particular pest we are considering and can therefore be assumed to be at demographic equilibrium. The forest ecosystem is therefore, described by a sixth-order nonlinear dynamical system: five equations describe the vegetation submodel, while the sixth one describes the population dynamics of defoliators.

It is practically impossible to detect all modes of behavior of such a complex model, if the parameters are not fixed or constrained to vary within 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 two of them, namely acidity of the deposition and maximum mortality inflicted by predators.

The paper is organized as follows: in Section 2 the model is described, and in Section 3 its possible modes of behavior are classified through bifurcation analysis. Catastrophic transitions and hystereses emerging from the analysis are illustrated in Section 4. Finally, results are discussed and possible refinements of the proposed model are suggested. The technical aspects of the bifurcation analysis are presented in Appendix.

2. THE MODEL

The dynamics of vegetation, in the absence of defoliators, is described by carbon and nitrogen exchanges 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. Under their assumptions, the model is described by the following differential equations with constant parameters

$$\dot{C}_{OV} = (a - bC_{OV})N_{OV} - mC_{OV} - \frac{v\alpha C_{OV}}{v\beta + C_{OV}}D$$

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

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

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

$$\begin{aligned} \dot{N}_{OV} &= -rmC_{OV} + g \frac{C_{OV}}{q + C_{OV}} \frac{N_{IS}}{h + N_{IS}} - \frac{v\alpha N_{OV}}{v\beta + C_{OV}} D \\ \dot{D} &= D \left(\varepsilon \frac{\alpha C_{OV}}{v\beta + C_{OV}} - \delta - \gamma D - \frac{\mu P}{\rho + D} \right), \end{aligned} \quad (1)$$

where “ $\dot{\cdot}$ ” indicates derivation with respect to time and the state variables are:

- C_{OV} = organic carbon contained in the foliage,
- C_{OS} = organic carbon contained in the soil,
- N_{OS} = organic nitrogen contained in the soil,
- N_{IS} = inorganic nitrogen contained in the soil,
- NOV = organic nitrogen contained in the foliage,
- D = biomass of defoliators;

all the parameters are nonnegative constants.

The model incorporates several phenomena that are hereafter described. The basic tenets are that nitrogen is the limiting nutrient for the production of vegetation biomass, while the activity of microbial decomposers is limited by the amount of carbon in the soil. We therefore restrict our attention to the foliage biomass, as organic nitrogen of vegetation is mostly contained in it (Sprugel, 1984) and the foliage, also rich in carbon, is the most readily decomposable vegetation component. The pest, by attacking the tree foliage, essentially depletes the vegetation compartments of organic carbon and nitrogen. Microbial decomposers in the soil mineralize organic carbon and nitrogen, which is then taken up by vegetation, and immobilize carbon and nitrogen in their biomass.

More in particular, in the equation for organic carbon in the vegetation we assume that shading reduces photosynthesis. This is translated into the term $(a - bC_{OV})N_{OV}$ with a being the production rate of vegetation biomass (measured in carbon) per unit of nitrogen contained in the vegetation, while b is the shading rate. Without defoliators the forest biomass would die off at a constant rate m ; the further mortality caused by defoliators is assumed to conform to a Holling type II functional response (Holling, 1965), in which α is the maximum input rate of foliage biomass (dry weight) per defoliator and β is the half saturation constant, namely the amount of foliage biomass at which the input rate is half the maximum. The amount of biomass input by defoliators is transformed into equivalent carbon units through v , the carbon content of foliage biomass (therefore, C_{OV}/v is the foliage biomass).

In the balance of organic carbon in the soil mC_{OV} is the flux of organic carbon due to dying vegetation, whereas,

if we call u the production rate of microbial biomass per unit of carbon, uC_{OS} is the amount of carbon immobilized in the microbial biomass per unit time. If e is the efficiency of microbial production, the amount of carbon input by decomposers is given by uC_{OS}/e and its difference with immobilized carbon yields the flux of mineralized carbon. A similar balance can be stipulated for organic nitrogen in the soil, provided one introduces two ratios nitrogen/carbon: r in the dead vegetation biomass and f in the microbial biomass. rmC_{OV} is thus the flux of organic nitrogen corresponding to dying vegetation and fuC_{OS} is the amount of nitrogen immobilized in the microbial biomass, while uN_{OS}/e is the amount of nitrogen input by microbial decomposers. The budgets of organic carbon and nitrogen in the soil are finally closed by considering that washout generate outflows $w_C C_{OS}$ and $w_N N_{OS}$ with w_C and w_N being the washout rates.

Meteorological precipitations, which contain the ions NO_3^- and NH_4^+ , affect the system by enriching the compartment of inorganic nitrogen (d is the corresponding inflow). On the contrary, leaching depletes the compartment (l is the leaching rate). Obviously, the flux of mineralized nitrogen which is subtracted from the balance of organic nitrogen is a positive contribution for this compartment, while the amount of nitrogen immobilized by microbes is a negative flux. Finally, the uptake of inorganic nitrogen by vegetation is modelled as the product of two Michaelis–Menten relationships. In fact, we have assumed not only that the uptake of inorganic nitrogen saturates with the concentration of inorganic nitrogen itself, but also that high values of vegetation biomass (expressed by C_{OV}) decrease the uptake of nitrogen per unit biomass. This is because with increasing biomass a greater part of production goes into bole and branches (rich in lignin) instead of foliage. In other words, the maximum flux g of inorganic nitrogen that vegetation can take up is multiplied by the product of two factors, which are both hyperbolic functions of respectively N_{IS} and C_{OV} (h and q are the corresponding half saturation constants).

The uptake of inorganic nitrogen is input to the compartment of nitrogen in the vegetation, which is depleted by both the decay of vegetation and the process of defoliation. Finally, the dynamics of defoliators includes the following phenomena (see Muratori and Rinali, 1989): the net production is proportional to ingested biomass through an ecological efficiency ε ; the baseline mortality δ of defoliators is increased by intraspecific competition for resources other than food (therefore, γD is the corresponding surplus mortality); the predators (described by their density P) cause further mortality,

which is modelled via a Holling type II functional response with μ being the maximum killing rate of defoliators per predator and ρ the half saturation constant, namely the biomass of defoliators at which the killing rate is half the maximum.

The influence of acidic deposition is not described in model (1), but can be incorporated as follows. Denote the flux of protons due to acidic deposition (inversely related to precipitation pH) with W and the concentration of protons in the soil (inversely related to soil pH) with Z . Z is in general an increasing function of W , although the degree of correlation greatly depends on the type of forest soil, in particular its buffer capacity. For this reason, we have treated W and Z as separate exogenous variables and supposed that:

— the flux d of inorganic nitrogen due to precipitation is an increasing function of W , in particular,

$$d = d_0 \left(1 + q_d \frac{W - W_0}{W_0} \right), \quad (2)$$

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;

— as foliage is damaged by acidity, the production rate a , and the mortality rate m of the vegetation biomass are decreasing and increasing with W , respectively;

— 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 take up is a decreasing function of Z , since roots are damaged by soil acidity;

— the half-saturation constant β in the defoliators' functional response 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 half-saturation constant, while W_C is the value of W where β is half the maximum; defoliators are, therefore, very sensitive to variations in acidic deposition just in the vicinity of W_C . This can be

TABLE 1

Dimensions, Ranges of Variability, and Reference Values for the Parameters Characterizing the Vegetation Submodel

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
v	kg (kg dw) ⁻¹			0.4
$u = u_0 \frac{1 - k_u Z/Z^*}{1 - Z/Z^*}$	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 · 10 ⁹
q	kgC ha ⁻¹	100	1000	300
h	kgN ha ⁻¹	0.1	100	1

Note. Reference is made to a forest of *Pinus sylvestris*. The parameter d depends upon W via Eq. (2).

justified by considering the effects of acid deposition on vegetation. There can be, for example, foliar damage resulting in erosion of the leaf cuticle whose integrity is a mechanism of resistance against defoliators. The increase in acidic deposition increases the density of points at which the resource can be successfully attacked by its consumers, so that β decreases, because the half-saturation constant is inversely proportional to the attack rate (Holling, 1965).

Table 1 summarizes the ranges of variability for the parameters of model (1) and their functional dependence upon the exogenous parameters W and Z . The values are typical for forests of Scots pine (*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 defoliators and predators are not given, because they are only roughly known.

3. MODES OF BEHAVIOR OF THE MODEL

In this section all asymptotic modes of behavior of model (1) corresponding to different values of W (flux of protons) and μP (maximum mortality inflicted by predators) are presented. This choice is motivated by the fact that the flux W of protons due to acidic deposition is the most interesting exogenous variable, while the predation mortality μP can be considered to a certain extent a variable characterizing different types of forests.

The results are based on a detailed bifurcation analysis of model (1) described in the Appendix and performed numerically by fixing defoliators and predators' parameters at the following reference values

$$\begin{aligned} \varepsilon &= 0.2, \quad \alpha = 20[\text{y}^{-1}], \quad \delta = 2[\text{y}^{-1}], \\ \rho &= 5[\text{kg ha}^{-1}], \quad \gamma = 0.02[\text{kg}^{-1} \text{ha y}^{-1}], \\ \beta_0 &= 5000[\text{kg ha}^{-1}], \quad W_C = 1[\text{keq ha}^{-1} \text{y}^{-1}]. \end{aligned}$$

The rationale behind these values is as follows: because of low assimilation rates, the gross production efficiency of herbivores very rarely exceeds 0.3; most pests are univoltine insects with a life span ($1/\delta$) of 1 year, the order of magnitude for ρ is comparable to that of defoliators biomass, namely a few kilograms per hectare; mortality γD due to intraspecific competition among defoliators is important (comparable to δ) for very high D (greater than 100 kg ha^{-1}); the order of magnitude of β , the half saturation constant of the defoliators' functional response, is comparable to the typical foliage

biomass; $W_C = 1$ corresponds to rain pH = 4 with a typical precipitation of 1 m per year; the maximum input rate of foliage biomass per defoliator α is such that, for high tree biomass, the defoliators population can increase. Moreover, it has been assumed that $q_d = 1$ in Eq. (2), i.e., a percent variation of the flux of protons W implies the same percent variation of the flux d of nitrogen (which is reasonable if the increase in acidic precipitation can be ascribed mainly to increase in NO_x emission).

After these premises, we can investigate the dynamical system behavior. With regard to the equilibria, there may exist two trivial equilibria; the first corresponds to absence of vegetation (and defoliators), which implies that nitrogen is present in the soil in inorganic form only ($\bar{N}_{IS} = d/l$), while the second corresponds to a pest-free forest at the asymptotic state set by the pollution load. This last equilibrium is denoted by $(\bar{V}, 0)$, where the vector

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

represents the equilibrium values of the five variables characterizing the vegetation submodel with the density D of defoliators set to zero. In addition to these two equilibria, there may exist strictly positive equilibria corresponding to forests infested by pests.

The trivial equilibrium $(\bar{V}, 0)$ (noninfested forest) exists (and is unique) when acidity of the rain (W) exceeds a threshold (rain is naturally acid and carries a certain amount of nutrients that are necessary for the survival of a forest), as proved in the Appendix where it is also shown that the equilibrium \bar{V} in the state space V of the vegetation submodel with $D = 0$ is stable. However, for suitable values of W and μP the equilibrium $(\bar{V}, 0)$ can become unstable in the whole space (V, D) of the system. In other words, for suitable values of the free parameters the defoliators can invade the noninfested forest.

The above results on the equilibria and the bifurcation analysis reported in Appendix are summarized in Fig. 1, where the parameter space $(W, \mu P)$ is partitioned into five regions, corresponding to five different asymptotic modes of behavior, indicated in the five corresponding windows of Fig. 1. In region [1], characterized by high pH values (i.e., low values of W) or high mortality μP inflicted by predators, the forest tends toward its pest-free equilibrium. In region [2], characterized by intermediate values of pH and predation mortality, the forest can be either infested or not and, depending upon the initial conditions, the system tends toward one of the two stable equilibria. In region [3], characterized by intermediate values of pH and small values of μP ,

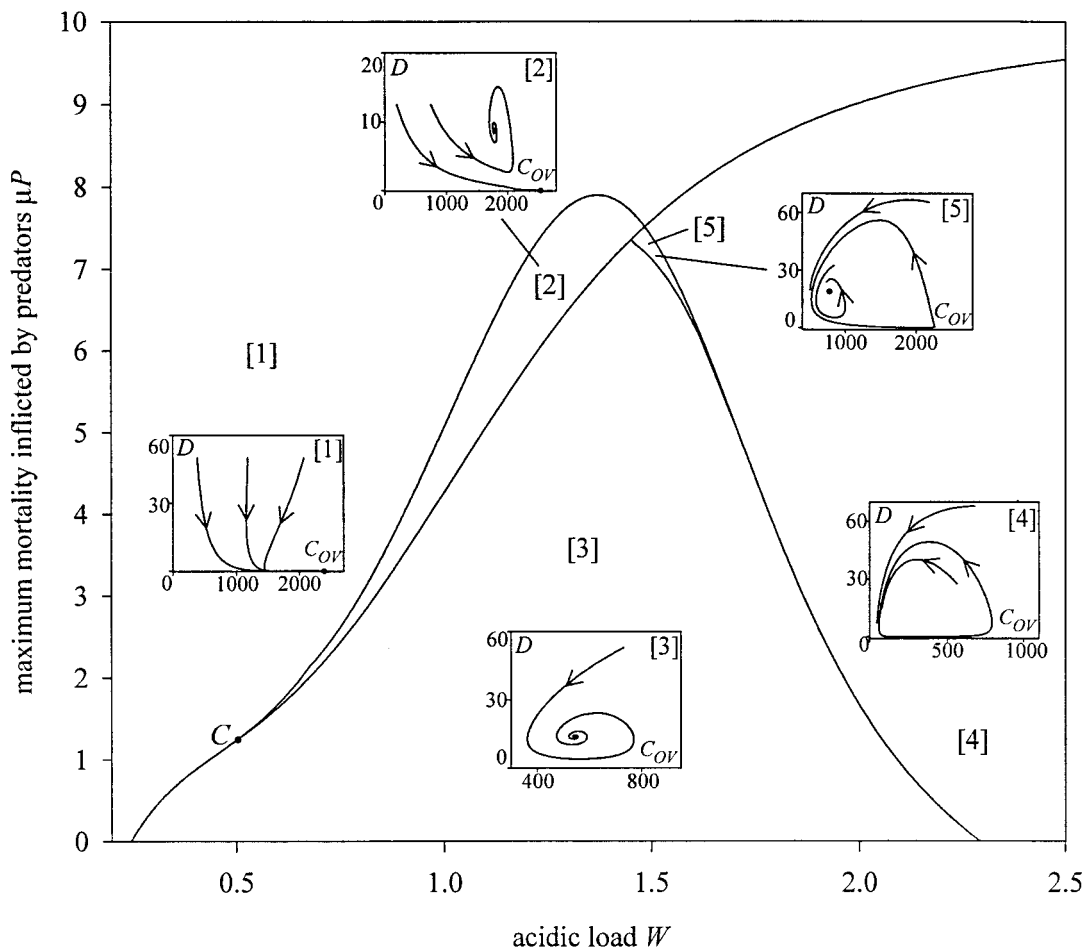


FIG. 1. Different modes of behavior of model (1) in the parameter space ($W, \mu P$). All curves are bifurcation curves (see Appendix). The asymptotic behavior in regions [1], [2], ..., [5] is indicated in the corresponding window. Parameters are at their reference values and: $W = 0.5, \mu P = 4$ (window [1]); $W = 0.95, \mu P = 4$ ([2]); $W = 1.5, \mu P = 4$ ([3]); $W = 2, \mu P = 4$ ([4]); $W = 1.48, \mu P = 7.3$ ([5]).

the forest is endemically infested. In region [4], characterized by very low pH values and low predation mortality, the forest is periodically infested (the most famous example of this kind of regime is that of the spruce budworm, *Choristoneura fumiferana*, for which several models have been devised, e.g., by Ludwig *et al.*, 1978; Antonovsky *et al.*, 1990; Rinaldi and Muratori, 1992). Figure 2 reports the cyclic evolution of vegetation and defoliator densities corresponding to three different points of region [4] and shows that the regeneration phase, during which the pest is barely detectable, can last a few decades, while the pest outbreak phase with the subsequent decline is about 10 years long. The figures are consistent with available data on pest-forest systems, e.g., those on the spruce budworm cycles in New Brunswick and Quebec in the past two centuries (Royama, 1984). Note that an increase in acidic load and/or predator density corresponds to an increase of the cycle period.

Finally, in region [5] the forest has a bistable behavior: it can be infested either periodically or at equilibrium. As in region [2], the attractor to which the system tends depends on initial conditions.

4. CATASTROPHES AND HYSTERESES

A more detailed analysis of Fig. 1 suggests further considerations. First of all, an increase of acidic deposition W , with a constant predator population P , can generate a transition from a noninfested to an infested forest. For example, if the system is at the trivial equilibrium $(\bar{V}, 0)$ (noninfested forest) in region [2], a small decrease of pH that implies crossing the curve separating regions [2] and [3] would elicit a transition ending with an infested

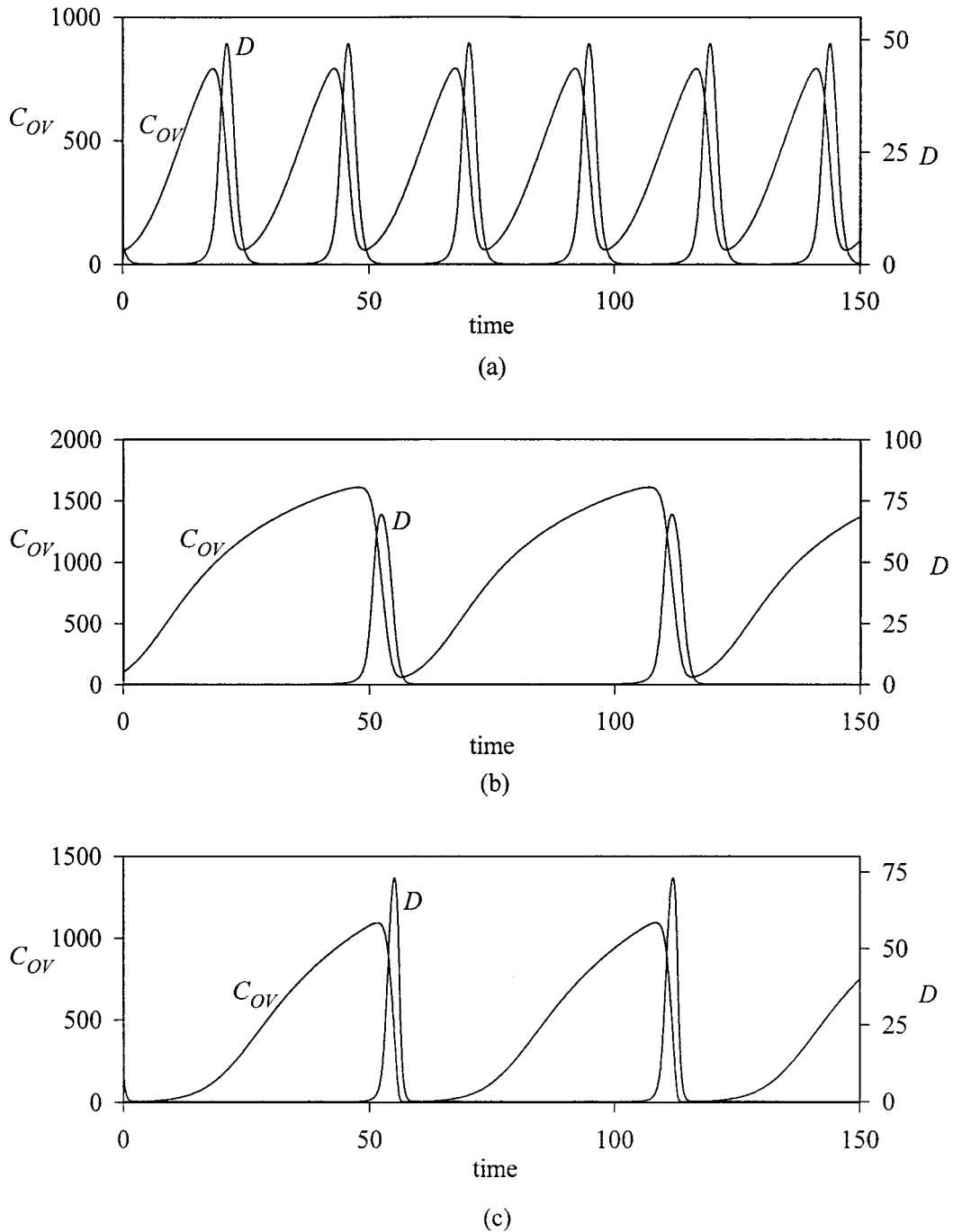
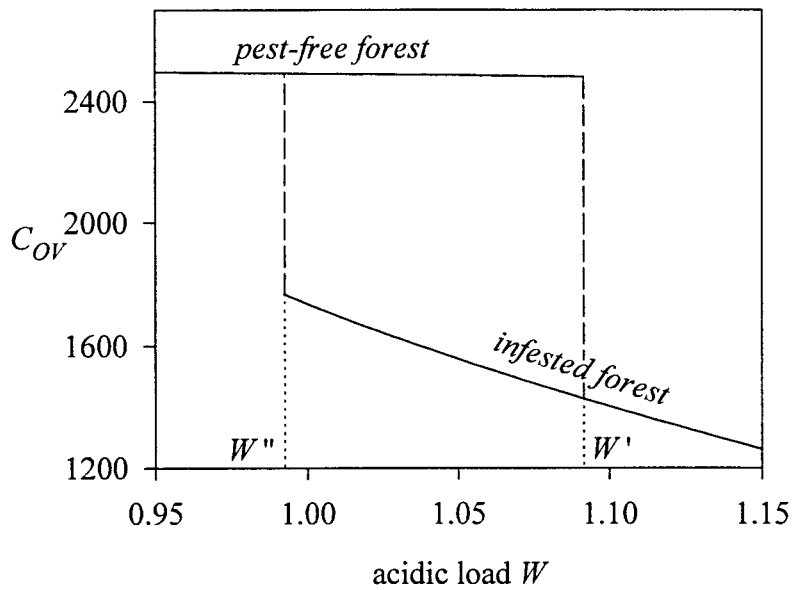
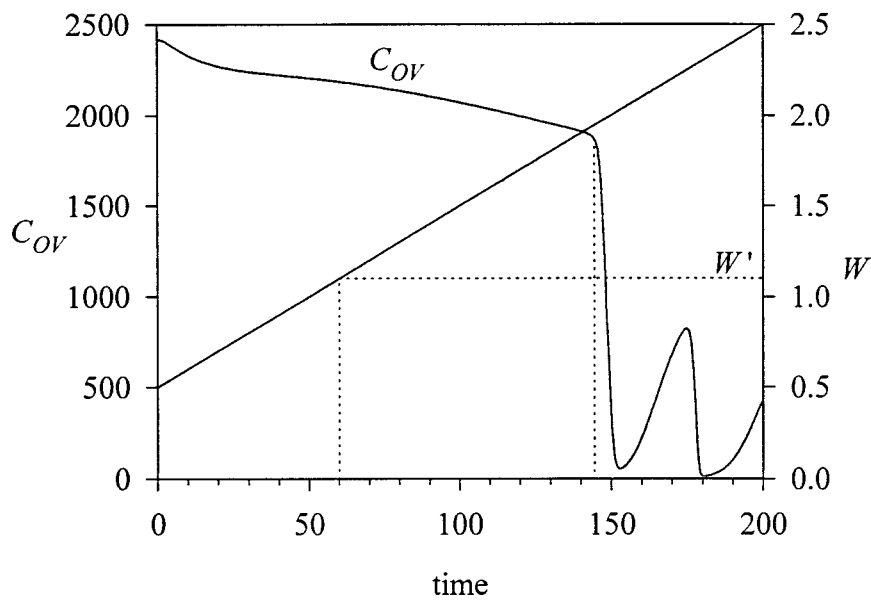


FIG. 2. Time [years] evolution of vegetation density (measured by C_{OV} [kg ha^{-1}]) and defoliators biomass (D [kg ha^{-1}]) for the reference parameter values in three different points of region [4]: (a) $W=2$, $\mu P=4$; (b) $W=2$, $\mu P=7$; (c) $W=2.5$, $\mu P=4$.



(a)



(b)

FIG. 3. (a) Vegetation density (measured by C_{OV}) at equilibrium as a function of acidic load for the reference parameter values and $\mu P = 5$. The dashed lines corresponding to W' and W'' indicate catastrophic transitions; the upper solid line refers to a pest-free forest, the lower to an infested one. (b) Response of vegetation density (measured by C_{OV}) to a continuous increase of acidic load (parameters are at their reference values and $\mu P = 5$). The plot is obtained by introducing a small amount of defoliators ($D = 10^{-2}$) in a forest at its carrying capacity and by linearly increasing the flux of protons W from 0.5 to 2.5 over 200 years. After 60 years the flux of protons reaches the critical value W' indicated by the hysteresis in (a) while the actual catastrophic transition occurs only after 140 years.

forest. Moreover, the bifurcation analysis reported in the Appendix shows that this transition is actually catastrophic, i.e., the state of the ecosystem varies macroscopically for a microscopic variation of pH. But catastrophic transitions are also possible as pH increases, moving from region [2] to region [1]. In this case, an infested forest will switch to a noninfested one and the catastrophe will actually correspond to forest regeneration.

The existence of catastrophic transitions in both directions with respect to W is a so-called *hysteresis* between two equilibria (the noninfested and infested forest). Figure 3a shows this hysteresis in terms of vegetation density. The upper solid line corresponds to the forest at its asymptotic biomass without defoliators, the lower one to the infested forest. A very slow periodical variation of acidic load encompassing the two critical values W' and W'' would, therefore, result in a hysteretic cycle between the two equilibria. Obviously, the real dynamic behavior of model (1) subject to a time varying acidic load W is different from that indicated by the hysteresis shown in Fig. 3a which refers only to equilibria. Figure 3b displays one possible scenario, obtained via a simulation in which a small amount of defoliators is initially introduced in a noninfested forest at equilibrium and the flux of protons W is continuously increased (from 0.5 to 2.5, which corresponds to a pH decrease from 4.3 to 3.6 when the precipitation is about 1 m y^{-1}) over 200 years. The higher critical value W' of Fig. 3a hysteresis suggests that the noninfested forest should be invaded by defoliators after 60 years (see Fig. 3b) while the simulation shows that the actual collapse occurs only after 140 years. The reason for this discrepancy is that the increase of W , slow as it may seem, is relatively fast if compared to the forest time constants.

It is important to remark that the transition from noninfested to infested forest due to an increase of acidic load, as well as the reverse transition, can also be a smooth decline, not involving catastrophes. This happens in forests with low density of predators, namely when an increase of W brings the systems directly from region [1] into region [3]. The biological interpretation of this result is the following. The presence of a great number of insectivores (above point C in Fig. 1) can keep the pest under control even when the damage produced by air pollution would favour the growth of defoliators. However, when a threshold value is exceeded, each extra unit of pest is fully uncontrolled, because of the limited killing rate of the predator, and can therefore give rise to a demographic explosion (catastrophe). By contrast, if birds and small mammals are not too many (i.e., below point C) and acidity increases slowly, then the pest can

gradually profit from the increasing damages of pollution to the foliage and smoothly increase its density.

5. CONCLUDING REMARKS

In this paper we have tentatively investigated the impact of acidic deposition on forest ecosystems by means of a mathematical model (Eq. (1)) in which the vegetation growth is described by carbon and nitrogen exchanges with soil. The aim of the study has been not to detail the demography and ecology of a specific forest, but rather to unravel the rich dynamical behaviors of a generic forest subject to both acidic precipitation and pest attack. For this reason, we have not used one of the currently available forest simulators, but have proposed a model which is a compromise between mathematical tractability and realism. The analysis of the bifurcations of this model has allowed the classification of possible forest functioning: (i) pest-free or infested; (ii) stationary or cyclic, and the classification of the nature of the impact of an increase of acidic deposition (a smooth decline or a dramatic collapse from a pest-free to an infested forest). The results reported in Fig. 1 show that a possible way to temporarily avoid damages to the forest is to compensate the increase of acidity by releasing predators of defoliators. The same figure also shows that drops in the predator population controlling the pest can also induce catastrophic transitions from pest-free to infested forest and that this is more likely to occur if rain pH is low. It is worthwhile to remark that, although the bifurcation analysis was carried out with respect to only two out of the many parameters defining the model, we have systematically checked that perturbations of the other parameters do not qualitatively alter the bifurcation diagram.

The results of the analysis presented in this paper are in qualitative agreement with those obtained by Muratori and Rinaldi (1989) with a naive model (logistic equation for the vegetation growth). Nevertheless, the analysis presented in this paper is more realistic, because the vegetational model is considerably more accurate. Also, the discussion of the catastrophes induced by variations of acidic load and predation pressure on defoliators is much more detailed. For these reasons we believe that the conclusions obtained with the present model are quantitatively reasonable, at least if order of magnitudes are considered. The simulation of a gradual increase of acidic load (Fig. 3) demonstrates that there might be long-term effects of increasing air pollution. The stress can be accumulated for a long time and suddenly be released without important warning signals, in the

matter of few years. The collapse can occur later than expected from simple steady-state analysis.

In the present paper, the parameter values of the model make reference to a hypothetical forest of *Pinus sylvestris*; but they could be suitably modified to study other kinds of forests. Also, the functional form of the equations, or the structure of some compartments, could be modified, to take care, for example, of tree age structure and defoliator stage structure (even if this would increase the model complexity and possibly hamper an analytical approach). In particular, it would be interesting to know if, by tuning the model to other forest ecosystems, one could also detect chaotic behavior. Indeed, this would support the idea that the randomness of the recurrent pest outbreaks observed in nature is, at least to a certain extent, due to interactions among the different compartments of the ecosystem and not only to environmental variability.

APPENDIX

This Appendix is devoted to the proof of the uniqueness and stability of the vegetational equilibrium state \bar{V} in the five-dimensional space characterizing the vegetation model and to the presentation of the bifurcation analysis of model (1).

Equilibrium \bar{V}

By annihilating the right-hand sides of model (1) with $D = 0$ and $\bar{C}_{OV} \neq 0$, and rearranging the equations, one obtains

$$\begin{aligned}\bar{C}_{OV} &= \frac{g}{rm} \frac{\bar{N}_{IS}}{h + \bar{N}_{IS}} - q \\ \bar{N}_{OV} &= \frac{m\bar{C}_{OV}}{a - b\bar{C}_{OV}} \\ \bar{C}_{OS} &= \frac{m\bar{C}_{OV}}{w_C + u(1/e - 1)} \\ \bar{N}_{OS} &= \frac{rm\bar{C}_{OV} + fu\bar{C}_{OS}}{w_N + u(1/e)} \\ \frac{w_N}{w_N + u/e} \left(r + \frac{fu}{w_C + u(1/e - 1)} \right) \\ &\times \left(\frac{g}{r} \frac{\bar{N}_{IS}}{h + \bar{N}_{IS}} - qm \right) = d - l\bar{N}_{IS}.\end{aligned}\quad (A1)$$

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

If

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

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

$$\frac{g}{rm} \frac{d}{hl + d} = q. \quad (A2)$$

By taking into account the dependence of g and d upon Z and W (see Table 1), Eq. (A2) can be solved with respect to W , thus giving a threshold for the proton load, below which vegetation cannot exist. By contrast, for W above the threshold, the equilibrium $(\bar{V}, 0)$ exists. Moreover, the stability of \bar{V} in the five-dimensional space characterizing the vegetation model can be proved by means of specialized software for algebraic manipulation applied to the Jacobian matrix evaluated at \bar{V} .

Bifurcation Analysis

The relationships among parameters characterizing the bifurcations of model (1) 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 is possible to numerically detect almost all bifurcations characterizing system (1) and to display them in any two-dimensional parameter space. In the following the bifurcation curves are shown in the parameter space $(W, \mu P)$.

Figure 4 is the bifurcation diagram in the parameter space $(W, \mu P)$ corresponding to the parameter setting specified in the text. The threshold value of W , below which vegetation is absent (see Eq. (A2)), does not appear in this figure because it is much smaller than 0.2. In this diagram there are several bifurcation curves, identified by one of the following symbols:

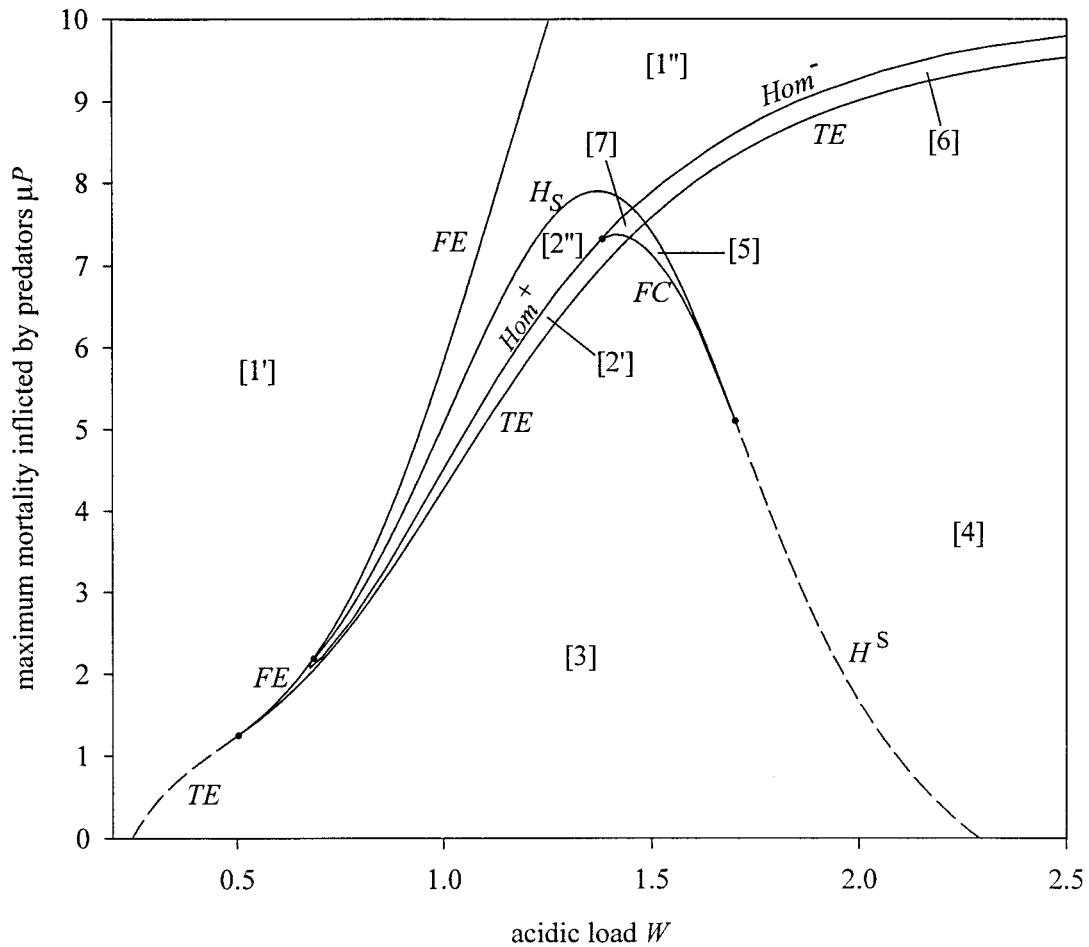


FIG. 4. Bifurcation diagram of system (1) with respect to acidic load W ($\text{keq ha}^{-1} \text{y}^{-1}$) and predator mortality μP ($\text{kg ha}^{-1} \text{y}^{-1}$) (other parameters are set to their reference values). TE , FE , H^S , H_S , FC , Hom^- , and Hom^+ indicate, respectively, transcritical bifurcation of equilibria, fold bifurcation of equilibria, supercritical and subcritical Hopf bifurcations, fold bifurcation of cycles, homoclinic bifurcations of stable and saddle cycles. Dashed curves are noncatastrophic bifurcations, while the others are catastrophic. Numbers and superscripts mark regions with the same set and type of invariants (see Table 2). For sake of comprehension, regions [2'], [6], and [7] have been made bigger than they actually are.

- TE , transcritical bifurcation of equilibria
- FE , fold bifurcation of equilibria
- H^S , supercritical Hopf bifurcation
- H_S , subcritical Hopf bifurcation
- FC , fold bifurcation of cycles
- Hom^- , homoclinic bifurcation for stable cycles
- Hom^+ , homoclinic bifurcation for saddle cycles.

The dashed curves are noncatastrophic bifurcations, while the others are catastrophic. All these bifurcation curves have been produced by LOCBIF, except the homoclinic curves Hom^- and Hom^+ which have been obtained by simulation after their existence has been ascertained by applying the theory exposed in Champneys and Kuznetsov (1994). The bifurcation

curves are the boundaries of different regions, indicated by [1'], [1''], ..., and [7] and characterized by a particular set of invariants (equilibria and cycles) as shown in Table 2. For all parameter values, there exists the trivial equilibrium $\bar{N}_{IS} = d/l$, $\bar{C}_{OV} = \bar{C}_{OS} = \bar{N}_{OV} = \bar{N}_{OS} = \bar{D} = 0$ (absence of vegetation and defoliators), which is always a saddle, while for each region, Table 2 specifies if the invariants are attractors, saddles, or repellers. The same number (irrespective of the superscript) has been attributed to regions characterized by the same attractors: for example, in regions [1'] and [1''] there is only one attractor, which is the trivial equilibrium $(\bar{V}, 0)$ (noninfested forest). For graphical reasons, regions [2'], [6], and [7] have been magnified; in fact, curves Hom^- and Hom^+ almost coincide with curves TE and FE . Figure 1 reported in the text is a

TABLE 2

Nonnegative Invariants for Each Region of Fig. 4

Region	Invariant	Type
[1']	Trivial equilibrium (\bar{V} , 0)	Attractor
[1'']	Trivial equilibrium (\bar{V} , 0)	Attractor
	Positive equilibrium	Saddle
	Positive equilibrium	Saddle
[2']	Trivial equilibrium (\bar{V} , 0)	Attractor
	Positive equilibrium	Attractor
	Positive equilibrium	Saddle
[2'']	Trivial equilibrium (\bar{V} , 0)	Attractor
	Positive equilibrium	Attractor
	Positive equilibrium	Saddle
	Cycle	Saddle
[3]	Trivial equilibrium (\bar{V} , 0)	Saddle
	Positive equilibrium	Attractor
[4]	Trivial equilibrium (\bar{V} , 0)	Saddle
	Positive equilibrium	Saddle
	Cycle	Attractor
[5]	Trivial equilibrium (\bar{V} , 0)	Saddle
	Positive equilibrium	Attractor
	Cycle	Saddle
	Cycle	Attractor
[6]	Trivial equilibrium (\bar{V} , 0)	Attractor
	Positive equilibrium	Saddle
	Positive equilibrium	Saddle
	Cycle	Attractor
[7]	Trivial equilibrium (\bar{V} , 0)	Attractor
	Positive equilibrium	Attractor
	Positive equilibrium	Saddle
	Cycle	Attractor
	Cycle	Saddle

Note. Each region contains also the trivial equilibrium $\bar{N}_{JS} = d/l$, $\bar{C}_{OV} = \bar{C}_{OS} = \bar{N}_{OV} = \bar{N}_{OS} = \bar{D} = 0$ (absence of vegetation and defoliators), which is always a saddle.

biologically meaningful compendium of Fig. 4. Regions [1'] and [1''], as well as regions [2'] and [2''] of Fig. 4, have been lumped together, as they correspond to the same attractor (see Table 2), while regions [6] and [7] have been eliminated because they are very small.

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