

Catastrophic bifurcations in a second-order dynamical system with application to acid rain and forest collapse

Simona Muratori and Sergio Rinaldi

Centro Teoria dei Sistemi, CNR, Politecnico di Milano, Milan, Italy

In this paper we present a second-order nonlinear dynamical system modelling the interactions of trees and damaging insects in a forest. With this model we discuss the influence of acidic deposition, an increase of which can cause sudden insect infestations and the collapse of the forest ecosystem. The analysis is carried out by finding the bifurcations of the system and by proving that under suitable conditions, such bifurcations can be catastrophic. The conditions for bifurcation can be explicitly given, and this facilitates the biological interpretation of the results.

Keywords: nonlinear systems, bifurcations, catastrophes, multiple equilibria, limit cycles, acid rain, forest collapse

Introduction

The increase in acidic deposition during the last decades has caused great damage in many forest ecosystems, in particular in the northern countries. Statistical evidence in the field data, laboratory experiments, and principles of biochemistry have allowed scientists to identify or, better, conjecture potential mechanisms through which an increase in acidic deposition might affect a forest ecosystem (see, for instance, Refs. 1 and 2 for comprehensive reviews). In general, these conjectures are not formally stated and make reference only to simple diagrams obtained through linear regression. It is therefore impossible, or at least very risky, to make any sort of quantitative forecast of the behavior of a given forest. Even predicting the kind of impact one should expect—namely, a smooth decline or a collapse of the forest—is a very difficult task. In other words, generic statements such as “in the next few years, damage to the leaf cuticle will become more and more frequent, and forest biomass will smoothly decrease” or “in the near future we will experience an unexpected and dramatic collapse of the forest” can hardly be supported scientifically.

We should first cast what we know of forest biochemistry into a mathematical model describing the dynamics of the ecosystem and then analyze such a model, in particular with regard to bifurcations.³ Only in this way can one really determine whether a series

of conjectured mechanisms can allow the prediction, or at least the explanation, of a forest collapse, which is nothing but the transition from an equilibrium (the healthy forest) that has become unstable to a new stable mode of behavior (the damaged forest).

The preceding arguments suggest that it is worth the effort to transform the most credited hypotheses about the potential mechanisms of impact of acid deposition on forests into mathematical models. The analysis of these models, which are in general deterministic dynamical systems, and in particular the nature of the bifurcations involving the parameters related to acidic deposition will give rise to a very interesting classification of many, if not all, impact mechanisms. To a first class (noncatastrophic bifurcations) belong those mechanisms that can cause only the smooth decline of a forest. Of course, in practice the decline can be quite consistent if acidic deposition increases at a high rate, but what is important in this context is that the forest will change its state gradually, say at the same speed as acidic deposition. Another class (catastrophic bifurcations) comprises the most dangerous mechanisms of impact, namely, those that can generate a discontinuity in the state of the forest. Of course, for technical reasons the analysis of the bifurcations is possible only if the models are fairly simple. This is why the first steps along this line,^{4,5} as well as the analysis presented in this paper, make use of low (second or third) order models. This method implies that only the main characteristics present in the ecosystem (such as trees, parasites, predators, toxic substances in the soil, and exploiters) are taken into account in modelling the forest and that “details” such as soil heterogeneity, species diversity, age structure of the trees, and variability of the climate are simply neglected. Such a procedure,

Address reprint requests to Professor Rinaldi, Centro Teoria dei Sistemi, Politecnico di Milano, Via Ponzio 34/5, 20133 Milan, Italy.

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which makes no sense when building a simulation model, is actually mandatory⁶ if one is trying to derive general principles and classify phenomena.

In this paper we propose a second-order nonlinear model that describes the interaction between trees and forest insects. As a matter of fact, the alterations to this interaction have been argued to be among the main causes of forest decline (see, for example, Chapter 14 of Ref. 1 and Chapter 4 of Ref. 2). Then we analyze the stability properties of such a model for all values of its parameters, assuming that the searching time of the damaging insect is the only biological parameter affected by acidic deposition. This might not be true in reality because acidic deposition also influences other parameters, but this is the only way to investigate whether such an elementary mechanism can by itself be responsible for the collapse of a forest. The analysis shows that, depending on the value of the other parameters, namely, depending on the kind of trees and insects, all cases are possible. In other words, forests of a certain type may be expected to decline with acidic deposition, while for other forests we should expect a collapse.

From a technical point of view the results are obtained by analyzing the qualitative behavior of a second-order nonlinear dynamical system. As far as we know, this system has never been studied, although it is a simple extension of two classes of systems recently considered by the authors.^{7,8} The system turns out to have multiple equilibria, the local stability of which can be easily discussed through the relevant Jacobian matrix. In some cases these equilibria are globally stable, while in other cases they are only locally stable or unstable (this happens, in particular, when there is a limit cycle that can be proved to exist for suitable values of the parameters). Moreover, analysis of the bifurcations shows that catastrophic bifurcations may occur and that the corresponding transitions in the state space can involve either two equilibria or one equilibrium and one cycle. The conditions for bifurcation can be explicitly given, and this facilitates the biological interpretation of the results.

The model

We now describe a forest model that accounts for the relationships between trees (x) and insects (y) in the presence of predators (e.g., birds) (z) feeding on the insects. In its essence this is a three-level food chain, $x \rightarrow y \rightarrow z$. For the reasons pointed out above, we assume that the territory under study is homogeneous, that age structure and species diversity do not influence the rate of growth of total tree biomass, and that climate and other environmental conditions are stationary. Moreover, we suppose that the predators can be approximated by a constant parameter (z). This is the case, for example, when predators are animals artificially controlled by humans or feeding also on resources other than y . Under these assumptions the dynamics of trees and insects is described by the following differential equations with constant parameters:

$$\dot{x} = rx \left(1 - \frac{x}{K} \right) - yp(x) \tag{1}$$

$$\dot{y} = y[cp(x) - d - ey] - zq(y) \tag{2}$$

where $x(t)$, $y(t)$, and z are suitable measures of density or biomass for trees, insects, and predators, respectively. In the absence of insects the rate of growth of trees per unit of biomass, namely, $r(1 - x/K)$, decreases with x . This is the standard assumption of logistic growth⁹ of resources, which, in the present case, accounts for competition of crowns for light and roots for nutrients. The intrinsic growth rate r describes the exponential growth $x(t) = x(0) \exp(rt)$ of the resource at low densities, while the carrying capacity K is the tree biomass at equilibrium in the absence of damaging insects (realistic values of r and K for various kinds of trees and soil at different latitudes can be found in specialized handbooks). The term $p(x)$ in (1) is the functional response¹⁰ of insects, namely, the tree biomass destroyed by each insect in one unit of time, and the parameter c in (2) is a simple conversion factor that specifies the birth rate of insects. The negative terms in (2) correspond to three different components of the mortality rate of insects: d is the baseline death rate per capita, namely, the death rate at low density and in the absence of predators; ey is the surplus of death rate due to intraspecific competition within insects; and $zq(y)$ is the mortality rate caused by predators.

To completely define our forest model, we must specify the functional responses $p(x)$ and $q(y)$. We do this by using the model proposed by Holling,¹⁰ which is by far the most commonly used in this type of study. Let us assume that the average distance between points at which the resource can be successfully attacked by insects (for example, erosion of leaf cuticles near trichomes and vascular tissues, lesions on lateral edges of leaves, and hypertrophy of mesophyll cells) is inversely proportional to tree biomass. Thus the "searching time," namely, the time the insect needs to find a unit of exploitable resource, is s/x , where s is a constant parameter. If the time h needed by each insect to handle one unit of resource is constant and all other activities of the insect occupy a fraction u of its time, we can write

$$\frac{s}{x}p(x) + hp(x) = 1 - u$$

from which it follows that

$$p(x) = \frac{b}{c} \frac{x}{a + x} \tag{3}$$

with

$$a = \frac{s}{h} \quad \frac{b}{c} = \frac{1 - u}{h}$$

Thus b/c is the maximum ingestion rate of each insect, and a is the half saturation constant, namely, the biomass of trees at which the ingestion rate of the insect

is half the maximum. In a similar way, one can derive the functional response $q(y)$ of predators, which can be written as

$$q(y) = \frac{y}{f + y} \tag{4}$$

by selecting suitable units for z .

In conclusion, by taking equations (1)–(4) into account, the model can be written as

$$\dot{x} = x \left[r \left(1 - \frac{x}{K} \right) - \frac{b}{c} \frac{y}{a + x} \right] \tag{5}$$

$$\dot{y} = y \left[b \frac{x}{a + x} - d - ey - \frac{z}{f + y} \right] \tag{6}$$

where the eight parameters r, K, a, b, \dots, f are positive and

$$b > d + \frac{z}{f} \tag{7}$$

because the maximum birth rate b of insects must be greater than their mortality rate at low density ($y = 0$) in order to have a meaningful system. Model (5)–(6) is of the form

$$\dot{x} = xg(x, y) \tag{8}$$

$$\dot{y} = yh(x, y) \tag{9}$$

with $g(0, y)$ and $h(x, 0)$ bounded for $x \geq 0$ and $y \geq 0$. It is therefore a positive dynamical system, since $x(0), y(0) \geq 0$ implies that $x(t), y(t) \geq 0$ for all $t > 0$. Systems of this kind have been studied by Kolmogorov in a celebrated paper¹¹ and by many other authors. Under suitable conditions, system (8)–(9) can have only two modes of behavior, called Kolmogorov's modes: a globally stable equilibrium or a globally stable limit cycle. This property, which is sometimes taken as a dogma, is actually not satisfied by system (5)–(6), as we will see in detail in the next section. (This fact has already been proved⁷ for the special case $e = 0$.) Thus our model is much more complex than the standard prey-predator model ($e = z = 0$ in (5)–(6)), which has been extensively studied^{12–15} and has indeed only the two Kolmogorov's modes of behavior.

As a last point, we now specify how acidic deposition influences model (5)–(6). Since we want to study the impact that acid deposition has on tree biomass indirectly, through perturbations of the host-insect interactions, we assume that all the parameters characterizing the natural growth of trees and the behavior of insects and predators are constant. On the other hand, we assume that the density of points at which the resource can be successfully attacked by the insects is strictly increasing with acidic deposition. Evidence for this assumption can be found in the literature² and is due to the fact that alteration of tree morphology, physiology, metabolism, or chemistry by acidic deposition may predispose forest trees to enhanced pathogen or insect activity. In particular, such a predisposition may be caused by erosion of the cuticle, since

integrity of epidermal cells is critically important as a resistance mechanism against a variety of insects. Alteration of foliar volatile release as well as changes in leaf chemistry, especially those involving ethylene, may also have important implications for insects in finding hosts. Thus from the preceding discussion it follows that the searching time of the insect is the only factor affected by acidic deposition. In conclusion, only one parameter, a , varies with acidic deposition in model (5)–(6). Consistently, in the following, such a parameter will be assumed to be a strictly decreasing function of acidic deposition.

Modes of behavior

In this section we analyze and classify all modes of behavior of system (5)–(6). To do this, we exploit simple geometric properties of the isoclines $\dot{x} = 0$ and $\dot{y} = 0$.

Isoclines $\dot{x} = 0$

Imposing $\dot{x} = 0$ in (5), we obtain a trivial isocline, namely, $x = 0$, and a nontrivial isocline ($g(x, y) = 0$) that has the form

$$y = \varphi(x) = \frac{c}{b} r \left(1 - \frac{x}{K} \right) (a + x) \tag{10}$$

and is therefore a parabola passing through point $(K, 0)$.

Isoclines $\dot{y} = 0$

Imposing $\dot{y} = 0$ in (6), we obtain a trivial isocline, $y = 0$, and a nontrivial isocline ($h(x, y) = 0$) that has the form

$$x = \psi(y) = a \frac{(f + y)(d + ey) + z}{(f + y)(b - d - ey) - z} \tag{11}$$

Its intersection with the x -axis

$$\psi(0) = a \frac{d + z/f}{b - d - z/f} \tag{12}$$

is positive (see inequality (7)), while the derivative at that point

$$\psi'(0) = -ab \frac{z/f^2 - e}{b - d - z/f} \tag{13}$$

is negative if and only if (recall that (7) holds)

$$\frac{z}{f^2} > e \tag{14}$$

Moreover, $\psi(y)$ is convex because $\psi'' > 0$. In fact,

$$\psi'' = -\frac{h_{yy}}{h_x} + h_{xy} \frac{h_y}{h_x^2}$$

but $h_{xy} = 0$, so

$$\psi'' = -\frac{h_{yy}}{h_x}$$

and $h_x > 0$, while $h_{yy} < 0$. Finally, it is trivial to check that the isocline $x = \psi(y)$ goes to infinity when y tends

to the unique positive root Y (see (7)) of the second-order polynomial

$$ey^2 + (ef - b + d)y - f\left(b - d - \frac{z}{f}\right) = 0 \quad (15)$$

Because of their convexity the two nontrivial isoclines $y = \varphi(x)$ and $x = \psi(y)$ can have no, one, or two intersections in the positive quadrant, as shown in *Figure 1(i)*, *Figures 1(ii)* and *1(iii)*, and *Figures 1(iv)* and *1(v)*, respectively. (We do not detail the relationships among the parameters that correspond to each of these cases because they are of no interest in the following discussion.) In all five cases there are two trivial equilibria: the origin, which is always a saddle, and point $(K, 0)$ (trees at their carrying capacity and absence of insects), which can be either a stable node or a saddle. We now analyze cases (i)–(v), and we show that only the first three cases have global attractors.

Case (i)

In this case there are no positive equilibria, so the Poincaré theorem on the index of closed orbits³ allows the conclusion that limit cycles do not exist in the positive quadrant. But one can actually prove that point $(K, 0)$ is a global attractor in the first quadrant. In fact, trajectories starting from the right side of the isocline $x = \psi(y)$ cross that isocline in finite time ($\dot{x} < -\alpha < 0$ in that region) and never come back to it because $\dot{x} < 0$ in the neighborhood of $x = \psi(y)$. On the other hand, all other trajectories starting from strictly positive initial conditions are characterized by $\dot{y} < 0$ and must therefore tend to $(K, 0)$.

Cases (ii) and (iii)

In these cases the trivial equilibrium $(K, 0)$ is a saddle (easy to check), while numerical trials show that the positive equilibrium can be either stable (actually globally stable) (*Figure 1(ii)*) or unstable (*Figure 1(iii)*). Nevertheless, when the positive equilibrium is unstable (case (iii)), there is a limit cycle around it. The proof (a direct consequence of the well-known Bendixon-Poincaré argument) is as follows. Consider the closed line $OKPQ$ (see *Figure 2*) comprised of the horizontal straight line PQ and the segments of trajectories QO , OK , and KP , the last one being the separatrix associated with the positive eigenvalue of the saddle point $(K, 0)$. Trajectories starting inside the region cannot cross or tend toward its boundary (notice that $\dot{y} < 0$ on segment PQ) and cannot tend to the positive equilibrium because such an equilibrium is unstable. Therefore trajectories tend toward a limit cycle surrounding the equilibrium. Moreover, with the same argument used in case (i), one can prove that trajectories starting outside region $OKPQ$ enter through segment PQ in finite time, so the limit cycle is globally stable provided that it is unique. The formal proof of this last fact, based on the analysis of the geometric properties of a Lyapunov function, is quite complex and will be presented elsewhere. (The study of the much simpler case in which two parameters, namely, e and z , vanish has required an entire paper.¹⁵)

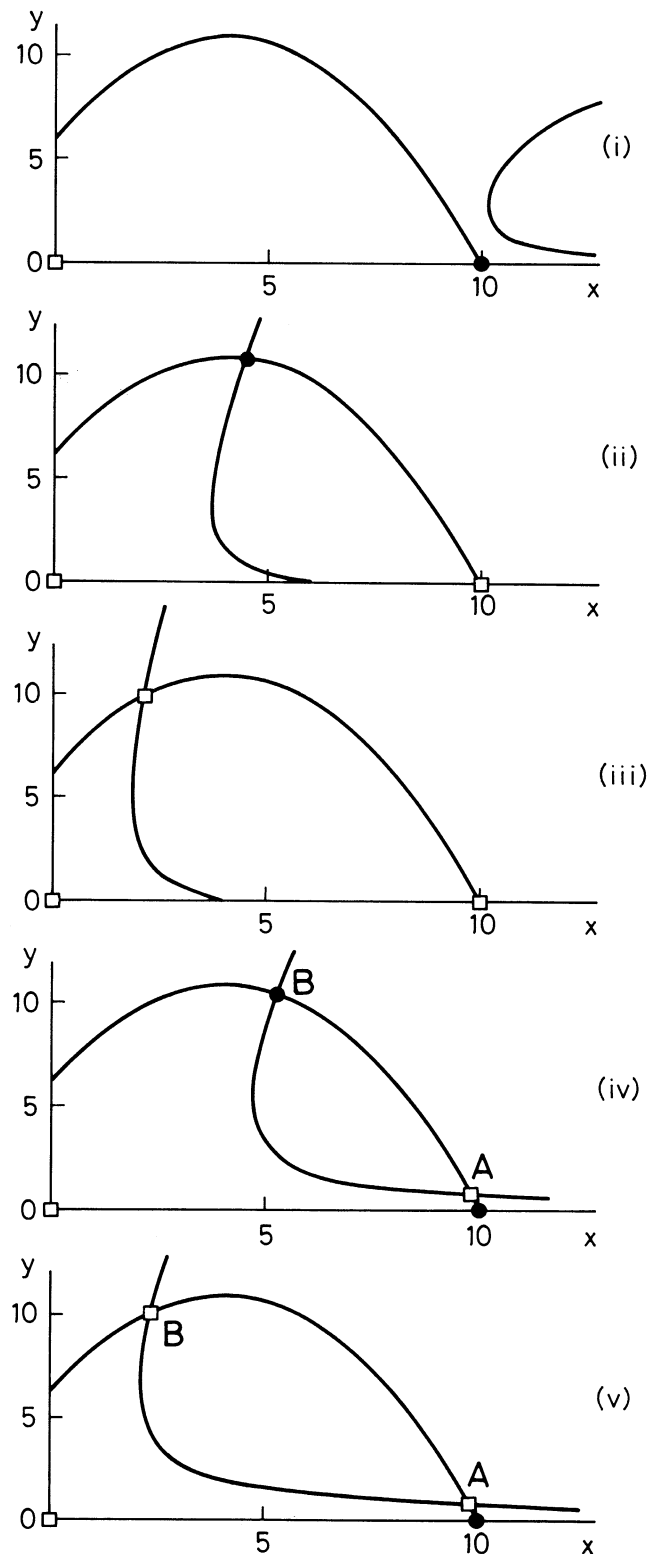


Figure 1. The nontrivial isoclines $y = \varphi(x)$, ($\dot{x} = 0$), and $x = \psi(y)$ ($\dot{y} = 0$) of system (5)–(6) in the five cases of interest. Open squares are unstable points, while solid circles are stable points. The graphs correspond to the following numerical values of the parameters: $r = 2$, $f = 1$, $K = 10$, $a = 2$, $e = 0.05$, $b/c = 2/3$, and $b = 5.1$, $d = 4$, $z = 0.5$ (case i); $b = 6$, $d = 3.5$, $z = 1$ (case (ii)); $b = 6$, $d = 2.2$, $z = 1.8$ (case (iii)); $b = 5.1$, $d = 3$, $z = 2$ (case (iv)); $b = 5.1$, $d = 2$, $z = 3$ (case (v)).

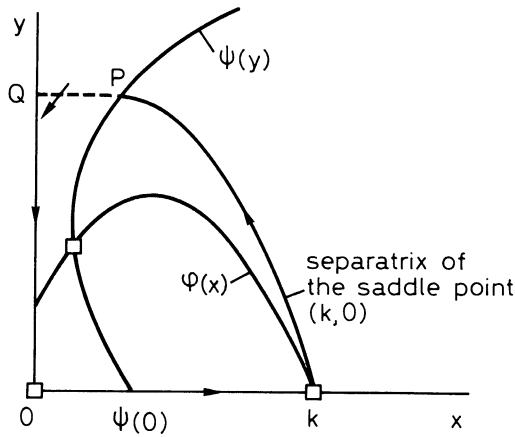


Figure 2. The nontrivial isoclines in case (iii) of Figure 1 and the Poincaré region OKPQ.

Cases (iv) and (v)

In these cases the trivial equilibrium $(K, 0)$ is a stable node, and one of the two positive equilibria (point A in Figures 1(iv) and 1(v)) is a saddle. In fact the Jacobian matrix at that point is given by

$$J = \begin{vmatrix} xg_x & xg_y \\ yh_x & yh_y \end{vmatrix} = \begin{vmatrix} -x\phi'g_y & xg_y \\ yh_x & -y\psi'h_x \end{vmatrix} \quad (16)$$

and its determinant

$$\det J = xyg_yh_x(\phi'\psi' - 1) \quad (17)$$

is negative, since $g_y < 0$, $h_x > 0$, and $\phi'\psi' > 1$. On the contrary, the second positive equilibrium can be either stable (point B in Figure 1(iv)) or unstable (point B in Figure 1(v)). Therefore in case (iv) we cannot have a global attractor because there are two stable equilibria. The same is true in case (v), in which there is a stable equilibrium and a stable cycle surrounding point B.

The above analysis shows that model (5)–(6) can actually fit the behavior of different types of forest. Case (i) is the most typical one: At equilibrium the trees are at their carrying capacity, and the damaging insects are absent (in practice they will be present at an endemic level). Any casual invasion of insects is absorbed, of course, with a more or less detectable but temporary decline of tree biomass (see Figure 3(i)). In case (ii), insects and trees coexist at an equilibrium that is still globally stable (Figure 3(ii)), while in case (iii) the forest undergoes periodic oscillations (Figure 3(iii)): A long period of tree growth is followed, all of a sudden, by an outbreak of insects and by the death of trees, after which the insects almost disappear and regeneration starts. This is what happens, for example, in the North American forests,¹⁶ where the principal tree species are birch, spruce, and balsam fir (in Ref. 16 a higher-order model is used that involves, nevertheless, a three-stage food chain (tree \rightarrow budworm \rightarrow birds)). Finally, cases (iv) and (v) correspond to forests with two locally stable modes of behavior (Figures 3(iv) and 3(v)). Indeed, the trees are at their carrying capacity if the insects are absent, but this equilibrium is only locally stable. After a small invasion of insects

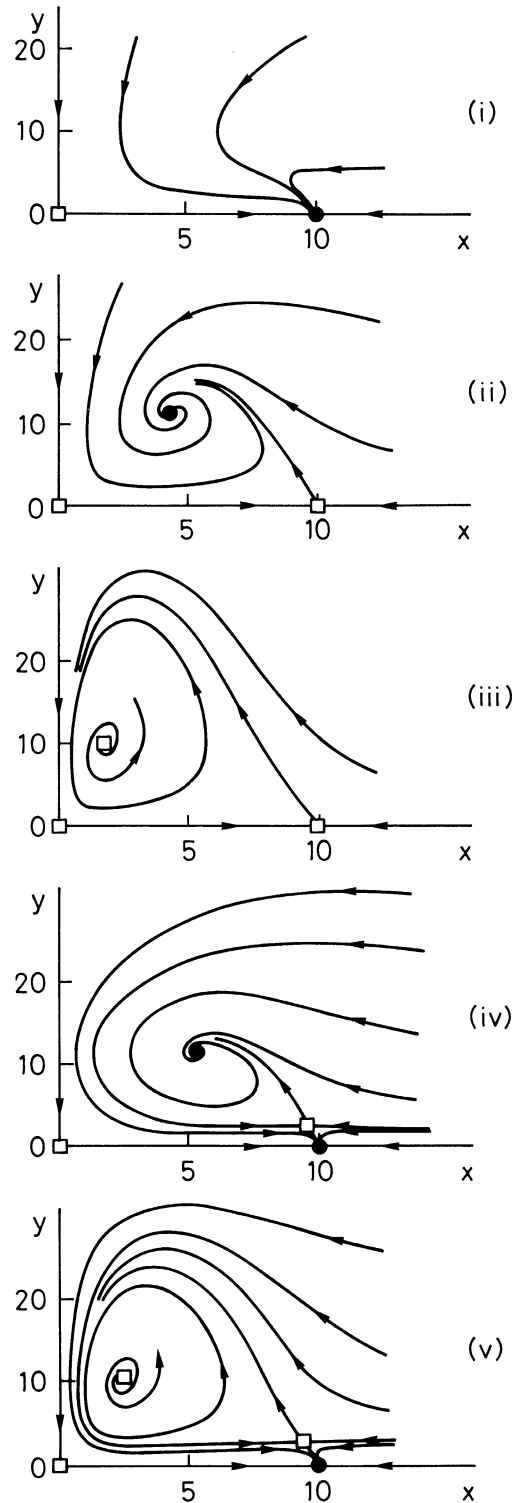


Figure 3. The trajectories of system (5)–(6) in the five cases considered in Figure 1.

the trees first decline and then recover to their carrying capacity. The same thing happens, but with a much longer and dramatic decline of the trees, if the invasion of insects is relevant. On the contrary, for intermediate initial values of y , the forest tends toward an equilib-

rium (Figure 3(iv)) or a cycle (Figure 3(v)) in which trees and insects find their way to coexistence. This kind of phenomenon is a typical feature of three-stage food chains⁷ and cannot be explained by simpler models.⁸

Catastrophic and noncatastrophic bifurcations

In this section we analyze the bifurcations involving the parameter a , which is the only one to be influenced by acidic deposition. Moreover, we concentrate our attention on the forests of the first type (case (i) in our preceding discussion). In other words, we assume that in normal conditions ($a = \bar{a}$) the forest has a globally stable equilibrium characterized by trees at their carrying capacity and absence of damaging insects (see Figure 3(i)). This choice is quite justified both biologically and mathematically.

When acidic deposition increases, the parameter a (initially equal to \bar{a}) decreases, and the two nontrivial isoclines $y = \varphi(x)$ and $x = \psi(y)$ are smoothly deformed. The parabola $y = \varphi(x)$ (see equation (10)) shrinks down as shown in Figure 4(a) (its derivative at point $(K, 0)$ is given by $\varphi'(K) = -cr(a + K)/bK$, and its second intersection with the x -axis is at point $(-a, 0)$). On the contrary the isocline $x = \psi(y)$ moves toward the left as indicated in Figure 4(b) (its intersection $\psi(0)$ with the x -axis (see (12)) as well as its derivative at that point (see (13)) are proportional to a , while its horizontal asymptote Y is not influenced by a (see (15)).

From the graphs of Figure 4 it is therefore clear that a bifurcation occurs when a equals that particular value, say a^* , for which the two corresponding isoclines intersect at point $(K, 0)$, that is, when $K = \psi(0)$. Thus from (12) it follows that

$$a^* = K \frac{b - d - z/f}{d + z/f} \tag{18}$$

and obviously $\bar{a} > a^*$ because we have assumed that in normal conditions ($a = \bar{a}$) the forest behaves as in Figure 3(i) ($\psi(0) > K$).

We can now study the nature of this bifurcation and find out when it is catastrophic and when it is not. We recall that a bifurcation is catastrophic when the stable equilibrium becomes unstable and no other stable equilibria or stable limit cycles can be found in its neighborhood. Thus a noncatastrophic bifurcation implies a continuous variation of the stable equilibrium (starting

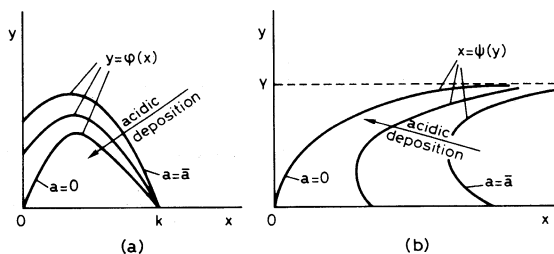


Figure 4. The influence of acidic deposition (parameter a) on the nontrivial isoclines $y = \varphi(x)$ (case a) and $x = \psi(y)$ (case b).

from point $(K, 0)$ after the acidic deposition has reached the critical value corresponding to $a = a^*$. On the contrary, if the bifurcation is catastrophic, when point $(K, 0)$ becomes unstable, the system will switch to a completely different mode of behavior. Therefore in the case of a noncatastrophic bifurcation the forest will simply decline, while in the opposite case it will collapse suddenly.

Noncatastrophic bifurcations

The condition for a noncatastrophic bifurcation at point $(K, 0)$ is

$$\frac{bK}{rc} \left(\frac{z}{f^2} - e \right) < 1 \tag{19}$$

In fact if (19) holds, we have (long but easy to check)

$$\varphi'(K)\psi'(0) < 1 \quad \text{for} \quad a = a^* \tag{20}$$

Thus in the neighborhood of point $(K, 0)$ the isoclines $y = \varphi(x)$ and $x = \psi(y)$ for $a = a^* + \epsilon$, $a = a^*$, and $a = a^* - \epsilon$ (ϵ small and positive) are shaped as in Figure 5: for $a = a^*$ the equilibrium $(K, 0)$ bifurcates into two equilibria, namely, $(K, 0)$ and (\bar{x}, \bar{y}) . The equilibrium (\bar{x}, \bar{y}) , which exists only for $Q = Q^* - \epsilon$, is always stable, since at that point the Jacobian matrix (16) has a negative trace ($\varphi' < 0$, $g_y < 0$, and y of the order of ϵ) and a positive determinant (17) ($g_y < 0$, $h_x > 0$, and $\varphi'\psi' < 1$ by continuity from (20)). On the contrary, the equilibrium $(K, 0)$ is stable for $Q = Q^* - \epsilon$, so the bifurcation is indeed noncatastrophic.

Catastrophic bifurcations

The condition for a catastrophic bifurcation at $a = a^*$ is just the reverse of (19), namely,

$$\frac{bK}{rc} \left(\frac{z}{f^2} - e \right) > 1 \tag{21}$$

In such conditions, $\varphi'(K)\psi'(0) > 1$ for $a = a^*$, and the two isoclines are shaped as indicated in Figure 6. Thus there are two equilibria (one of which is stable) for $a = a^* + \epsilon$ and one for $a = a^* - \epsilon$, so the bifurcation is catastrophic. In this case, when acidic deposition increases so much that a becomes smaller than a^* , the system will leave the equilibrium $(K, 0)$ and tend toward a positive equilibrium (in the case of Figures 1(ii) and 3(ii)) or toward a limit cycle (in the case of Figures

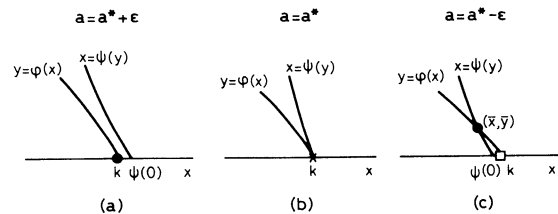


Figure 5. The nontrivial isoclines and the equilibria of system (5)–(6) in the case of a noncatastrophic bifurcation. (Open squares are unstable points, solid circles are stable points, and X' 's are critically stable points.)

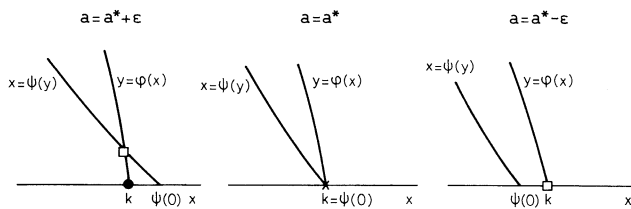


Figure 6. The nontrivial isoclines and the equilibria of system (5)–(6) in the case of a catastrophic bifurcation. (Open squares are unstable points, solid circles are stable points, and X's are critically stable points.)

1(iii) and 3(iii)). In any case, in a very short time the forest will be infested by insects, and tree biomass will be substantially reduced.

Discussion

The above analysis has shown that the simple forest model we have proposed can account for different kinds of behavior of forest ecosystems. In particular, the model explains the case in which damaging insects are present only at an endemic level as well as the case in which the forest is periodically infested by insects. But the most important result of the analysis is that our model can be used to discuss the influence of acidic deposition. In fact, in the case in which predisposition of forest trees to insect infestation is enhanced by acidic deposition, we have proved that the point at which the first impacts on tree biomass are detectable can be easily quantified by a simple formula (equation (18)). In particular, this formula says that the forests that should be affected first are those that have a large carrying capacity of the trees (K), a large maximum birth rate (b) and a low death rate (d) of the insects, and a low pressure of the predators on the insects (z small and f large). But the analysis can also distinguish between smooth impacts (decline of tree biomass) and dramatic impacts (collapse of the forest), again through a very simple formula (equation (19) or (21)) that qualifies the nature of the bifurcation. Such formulas, for example, state that a collapse is more likely in forests with low growth rate of the trees (r), high number of predators (z), and weak intraspecific competition within insects (e). Moreover, the comparison of equation (18) with equations (19) or (21) points out some very interesting facts, which could hardly be proved without the analysis of the bifurcations. For example, equation (18) shows that a possible way to temporarily avoid damages in a forest subject to increasing acidic deposition and potential pest infestation is to increase the number of predators (z) feeding on the insects (a^* decreases with z in (18)). But equation (21) shows that if z is increased, there are higher chances that the forest will collapse when it is finally affected. In other words, with this type of countermeasure (stocking the forest with predators) we can postpone the time of the impact but at the risk of transforming it in a real disaster. Similar phenomena have already been pointed out in forest management (for example, a number of artificial

countermeasures give rise to less frequent but more severe forest fires) and seem to be a typical product of the possibility of accumulating stress in a dynamical system, which is, after all, nothing but an interpretation of catastrophic bifurcations.

Concluding remarks

We have shown in this paper how one of the many conjectured indirect mechanisms of impact of acidic deposition on forests can be transformed into a mathematical model and how the analysis of the bifurcations of that model can allow the classification of the nature of the expected impact (a simple decline or a sudden collapse of the forest). The conditions for catastrophic bifurcations have been found explicitly so that interesting biological conclusions pointing out the role of different parameters (such as tree carrying capacity, number of predators, degree of intraspecific competition, and birth and death rate of the damaging insects) have been found. The analysis is only qualitative, since the model is oversimplified and the numerical values of the parameters are only roughly known. This situation calls for the refinement of the present model (for example, substitution of foliage, branches, and trunk biomass for tree biomass) and for a better knowledge (based on statistical analysis of available field data) of the numerical values of the parameters. Only when these conditions are satisfied can a qualitative theory like the one we have presented in this paper become quantitative and allow the prediction of time and type of impact on a forest ecosystem. But before going into more details in a single case, we believe it would be worth analyzing other major mechanisms of impact, with the same aim and style that we have used in this paper, in order to construct a simple but sound and complete theory for the impact of acidic deposition on forest dynamics.

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