



Catastrophes in Exploited Forests

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CATASTROPHES IN EXPLOITED FORESTS**

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ABSTRACT

(1) This paper shows why small variations of the human exploitation of a natural forest can give rise to dramatic changes in forest biomass.

(2) Two simple mechanisms for catastrophes, already pointed out for other ecosystems, are briefly discussed at the beginning of the paper. The first occurs when depensation phenomena are present in the forest growth curve, while the second is due to the concavity of the harvesting function, which can be interpreted as the functional response of the forest exploiters. In both cases a small increase in the exploitation can lead to the collapse of the forest.

(3) A more interesting mechanism for catastrophes is then presented. It is based on the dynamics of the soil nutrient and the fact that tree mortality may become very high when soil acidity exceeds a threshold.

(4) In particular, it is shown that an increase of the exploitation may give rise to a catastrophic collapse of the forest if the exogenous nutrient inflow (i.e., acidic deposition) is sufficiently high. Moreover, such a catastrophe is irreversible, i.e., reforestation is not possible, if the nutrient inflow is too high.

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CATASTROPHES IN EXPLOITED FORESTS

Marino Gatto and Sergio Rinaldi

1. INTRODUCTION

It is well-known that theory and observation indicate that some natural multi-species assemblies of plants and animals are likely to possess several different equilibrium points (see May 1977 for an interesting review). This implies that substantial external shocks (such as, for example, winds, fires, pests, or releases of toxic substances in the case of a forest) may perturb the ecosystem from a stable equilibrium into the region of attraction of another stable equilibrium. Thus, in these cases, the state in which the system is at a specified time strongly depends upon the time and amplitude of the past historical accidents. But the existence of multiple stable equilibria may also be the cause of more subtle and intriguing changes, called catastrophes, which are caused by a small variation of a parameter (see Sect. 2 for more details). Examples

of catastrophes have been reported, in general without using *catastrophe theory*, by many investigators. For example, Noy-Meir (1975) has pointed out that a discontinuous change in grazed vegetation may occur when the density of the herbivores smoothly increases; Clark (1976) has given a review of catastrophes in fisheries; Ludwig, Jones & Holling (1978) have shown why outbreaks of insect pests can occur when foliage biomass reaches a threshold.

In this paper we outline three possible mechanisms which cause catastrophic events in the dynamics of natural forests subject to human exploitation. Two such mechanisms have already been discussed by Clark (1976) and Noy-Meir (1975) with reference to other ecosystems and involve just the tree biomass dynamics and the specific mode of forest exploitation: the first is based on the inverse density-dependence in the relationship between the growth rate per unit biomass and the total biomass, while the second is related with the concavity of the harvesting function of the exploiters. The third mechanism is more complex and takes into account also the dynamics of the nutrients in the soil. In this case the forest collapse is based on the fact that tree mortality may become very high when soil acidity exceeds a given threshold. Since soil acidity depends upon the exogenous inflow of nutrient due to natural sources, fertilization and acidic deposition, also the possibility of collapse and of reforestation may depend upon such an exogenous inflow.

The mathematical models we use in this paper to carry out our analysis on forest dynamics are very crude. We take in fact a short-cut approach to the problem by lumping a lot of different phenomena into a single equation of tree growth. This simplicity, however, allows us to

detect the stability properties of all the equilibria of a forest ecosystem, a condition which is necessary to point out the potential catastrophes. It should be clear, however, that the aim of this work is only conceptual and qualitative (as any formal theory in ecology): our model is not meant to rival, on a quantitative ground, the complex and detailed simulation models that are currently built and used by the agencies responsible for forest management.

2. BACKGROUND ON CATASTROPHES

Although catastrophe theory (see Thom 1972, Zeeman 1977) has become quite fashionable and has already been used in ecology (see, for example, Jones 1977, Bazin & Saunders 1978, Casti 1982, Kempf, Duckstein & Casti 1984) we shortly recall what is meant by catastrophe in this specific context.

First of all we need to introduce as a basic ingredient a measure of the forest exploitation. This is a well-known concept and can be quantified in various ways, for instance, the percentage of standing trees that can be cut per year, or the amount of labor and capital employed in felling trees. If we look at the problem from a functional point of view, tree logging can be viewed as a human predation and exploitation can be interpreted as aggressiveness of the predator.

If exploitation is kept constant over time, the state of the system, i.e., the variables that characterize the problem (tree standing biomass, harvested biomass, nutrient concentration, etc.) will converge to one of the stable equilibria. When exploitation is smoothly and slowly increased also these equilibria will vary smoothly. But sometimes a small

(infinitesimal) perturbation of a parameter, the exploitation E in the case at hand, from a particular given value \bar{E} entails the appearance or disappearance of an equilibrium. In other cases, an equilibrium which is stable for $E < \bar{E}$ becomes critical for $E = \bar{E}$ and unstable for $E > \bar{E}$, or vice versa. Now, if we imagine that an exploited forest is in a stable equilibrium for $E < \bar{E}$ and that this equilibrium disappears or becomes unstable for $E > \bar{E}$, we can say that we have a catastrophe. In fact, as soon as the exploitation E is higher than \bar{E} , the state of the system moves toward a different stable equilibrium which can be quite far from the one in which the system was before the perturbation. This dynamic transition from one equilibrium to another is a catastrophe. The most spectacular catastrophes are the *collapse* of a forest and the sudden *bloom* of a deforested area.

3. GROWTH AND HARVESTING FUNCTIONS

Let $T(t)$ be the total tree biomass in the forest at time t . Then, if the forest is not exploited, the rate of change dT/dt of tree biomass is simply the natural growth rate G which is here assumed to be a function of tree biomass only, i.e.,

$$\frac{dT}{dt} = G(T)$$

In the normal compensatory case the growth rate per unit biomass $G(T)/T$ is a decreasing function of total tree biomass (density-dependency operates via increased mortality and/or decreased fertility) and $G(T)$ is concave as shown in Figure 1. Sometimes, however, crowding can be, within certain limits, not deleterious but favorable to the

well-being of each tree. For instance, Silvertown (1982) reports two studies on *Pinus ponderosa* which show that the probability of a seed escaping predation by chalcid wasps (Fowells and Schubert 1956) and by Abert squirrels (Larson and Schubert 1970) is an increasing function of the crop size. Therefore, the effect of density is contrary to usual (inverse density-dependence). In this case it is possible that the growth rate per unit biomass $G(T)/T$ is first increasing with T and then decreasing: this phenomenon is called *depensation*. When, in the limit, $G(T)$ is initially negative, the so-called *critical depensation* takes place. Thus, if there is depensation the natural growth rate $G(T)$ is first convex and then concave as shown in Figure 1.

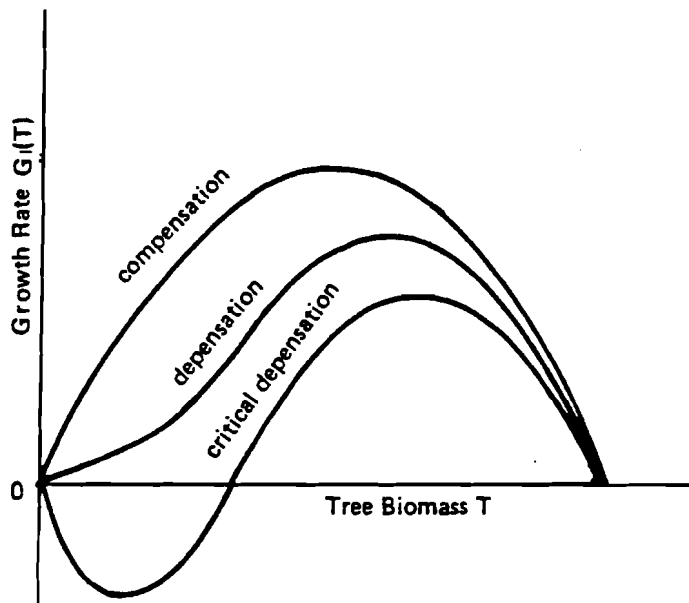


FIGURE 1. Different types of natural growth rate functions.

When the forest is exploited, the rate of change dT/dt of tree biomass is the difference between natural growth rate G and harvesting rate H . The harvesting rate may be quite different from case to case: it represents the management policy followed by the exploiters and reflects their attitude toward risks and benefits. In real world situations the rate of harvest H may be a rather complex function of age distribution, density, and current economic value of the trees present in the forest. Nevertheless, in order to describe the forest growth with a single equation we must assume that the harvesting rate H can be specified as a function of tree biomass only, i.e., $H = H(T)$. This function will be called *harvesting policy* in the following. Moreover, let us write

$$H(T) = E h(T) \quad (1)$$

where the *harvesting function* $h(T)$ describes the dependence of harvest upon biomass and the multiplicative parameter E , called *exploitation*, somehow represents the aggressiveness of the exploiters and hence the stress exerted on the forest. Variations over time of the harvesting policy $H(T)$ may be reflected into variations of the harvesting function $h(T)$ or into variations of the exploitation E . The last is the variation that, in accordance with catastrophe theory, is considered in this paper.

One way of keeping the forest biomass close to a desired equilibrium value \bar{T} is to avoid harvesting if the forest biomass T is smaller than \bar{T} and harvest at the rate $G(\bar{T})$ otherwise. Nevertheless, if such a harvesting policy is used, the unavoidable fluctuations of tree biomass around the equilibrium value \bar{T} induced by disturbances would imply very frequent switches from maximum production $\bar{H} = G(\bar{T})$ to no production at all. For this reason, smooth *sigmoid* harvesting policies like the one

corresponding to curve (a) of Figure 2 are certainly preferred. Another harvesting policy is related to the use of *percent quotas*, which means that a fixed percentage of the standing trees can be cut each year. In this case the harvesting policy is simply given by (see curve (b) of Figure 2)

$$H = ET \quad (2)$$

where the exploitation E is proportional to the percentage of standing biomass that can be harvested each year. Finally, we can also consider the case in which the parameter E represents, in suitable units, the amount of labor and capital invested in lumbering, for example, the number of workmen employed in felling trees. During the unit time interval each woodman can either search or cut or transport what is harvested. Therefore, if we denote by s the time for searching one unit of biomass, by c the time for cutting, by p the time for transporting and by h the woodman's harvest during the unit time interval, it is obvious that

$$(s + c + p)h = 1 \quad (3)$$

While c and p can be assumed to be constant, the searching time s is in general a function of tree density: the more dense the trees are, the faster the search is. If forest biomass and tree density are positively correlated, then a crude but reasonable assumption is

$$s = \frac{\alpha}{T} \quad (4)$$

where α is a positive parameter. Thus, from Eqs. (1), (3), and (4) we obtain

$$H = E h = \frac{ET}{\alpha + (c + p)T} \quad (5)$$

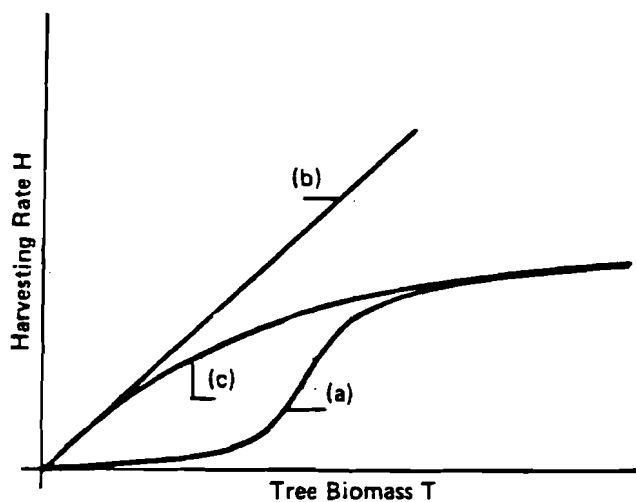


FIGURE 2. Different types of harvesting policies: (a) *sigmoid* (third type functional response); (b) *linear* (percent quotas); (c) *concave* (second type functional response).

which says that, for any given value of the exploitation, the harvesting policy is a *concave* saturating function of the tree biomass (see curve (c) of Figure 2). It should be remarked that Eq. (5) is nothing but the well-known *disc equation* introduced by Holling (1959) with reference to the phenomenon of predation. Our harvesting function $h(T)$ is what Holling terms predator's *functional response*. All this should not bring any surprise, since tree logging is nothing but a form of human predation.

4. TWO SIMPLE CATASTROPHES

Let us now consider the case of a forest with depensation and let us suppose that the harvesting policy is linear (see Eq. (2)), i.e.,

$$\frac{dT}{dt} = G(T) - ET$$

Thus, the steady states corresponding to different degrees of exploitation can easily be found by intersecting the growth function $G(T)$ with the straight lines through the origin (see Figure 3).

If the exploitation is low, i.e.,

$$0 < E < E' ,$$

where E' is equal to the derivative of the growth function at the origin (see Figure 3), there are two equilibria: the extinction (point 0) which is *unstable* and a non-trivial steady state (point 1) which is *stable*. For higher exploitation, i.e., when

$$E' < E < E''$$

where E'' is defined in Figure 3, a third intermediate unstable equilibrium (point 5) moves in, and extinction (point 0) becomes stable. Finally, if the exploitation is equal to E'' the two non-trivial equilibria (points 3 and 5) coincide, thus giving rise to a *critical* equilibrium (point 4), while if the exploitation is very high, i.e.,

$$E > E''$$

there is only one stable equilibrium, the extinction.

Correspondingly the mappings of the stable tree biomass T and of the harvest rate H versus exploitation are as shown in Figure 4. It is apparent that the values E' and E'' of the exploitation mark the appearance of a catastrophe. When the exploitation is slowly increased the tree biomass smoothly decreases (see points 1, 2, 3, 4 along the growth curve of Figure 3) until the critical value T'' is reached (see Figure 4). At that point if the exploitation is further increased, trees die and the forest collapses (recall that point 0 of Figure 3 is stable for $E > E''$). Now, if the

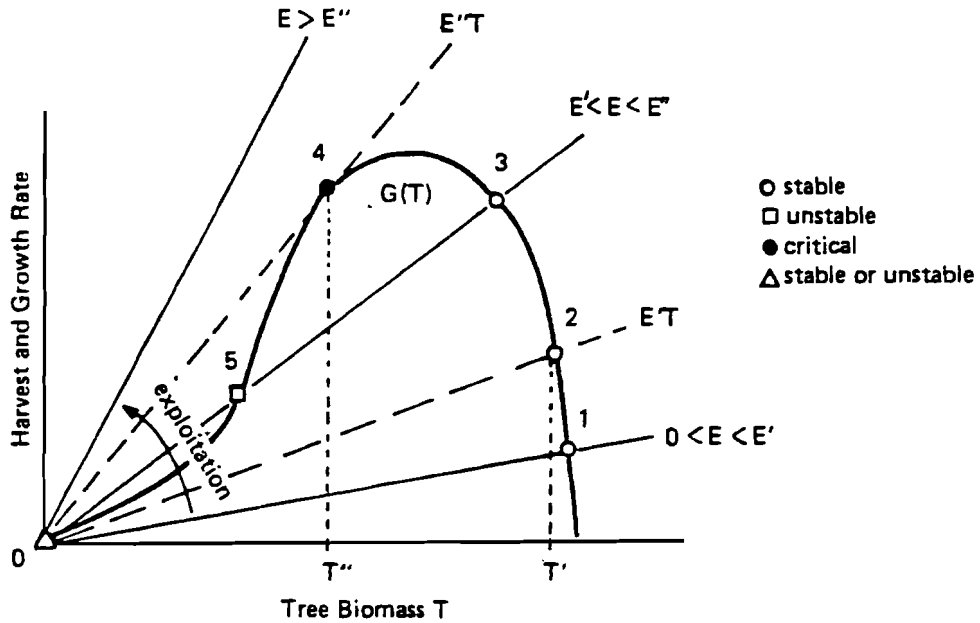


FIGURE 3. Depensation in the growth rate $G(T)$ and multiple equilibria.

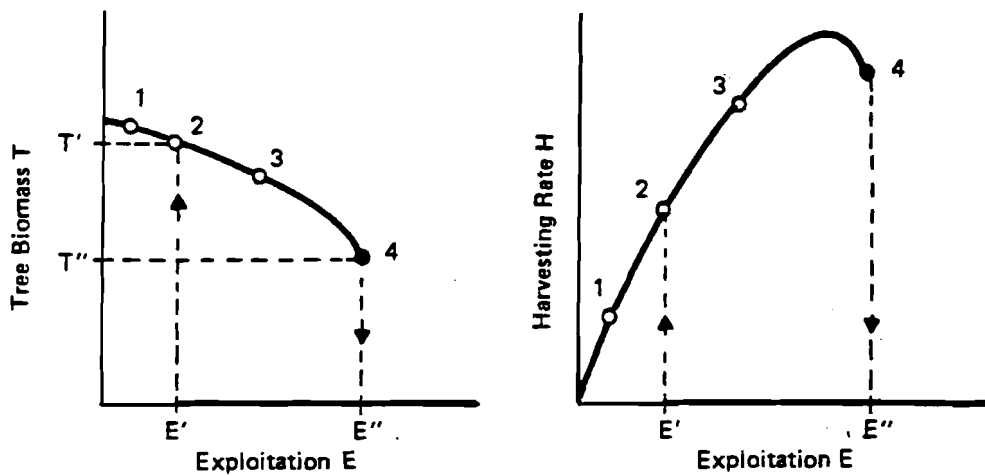


FIGURE 4. Tree biomass T and harvesting rate H vs. exploitation E when depensation is present. The values E' and E'' of the exploitation mark the critical values of the fold catastrophes. The points 1, 2, 3 and 4 are the same as in Figure 3.

exploitation E is reduced after the new equilibrium $T = 0$ has been reached or approached, trees do not grow any more unless exploitation is substantially decreased. In fact, only when E becomes smaller than the critical value E' point 0 in Figure 3 becomes unstable again and the tree biomass sharply increases toward the value T' (see Figure 4). This type of catastrophe, which essentially points out the existence of a *hysteresis*, is called *fold catastrophe*.

When denpensation is critical, extinction is always a stable steady state and this implies that the catastrophe is *irreversible*. In words, this means that in this case reforestation is not possible once the critical exploitation E'' has been exceeded.

It is important to notice that denpensation *per se* does not always give rise to catastrophes (the existence of a catastrophe is indeed related to the particular structure of the function $G(T) - E h(T)$). In fact, catastrophes can be avoided even in the presence of denpensation (see Figure 5) provided harvesting is prohibited when the forest biomass is below a threshold value T^* , i.e.,

$$H(T) = \begin{cases} 0 & \text{if } T \leq T^* \\ E(T - T^*) & \text{if } T > T^* \end{cases}$$

Harvesting policies of this type make sense in practice, because too low harvesting is often not economically acceptable. Indeed, if the fixed costs for harvesting are higher than the profits when the harvest rate is lower than a prescribed value H^* , then no harvest should take place if $T < T^*$, where T^* is such that $G(T^*) = H^*$. Therefore, provided T^* is sufficiently high (as in Figure 5), we have found an example in which economics implies conservation.

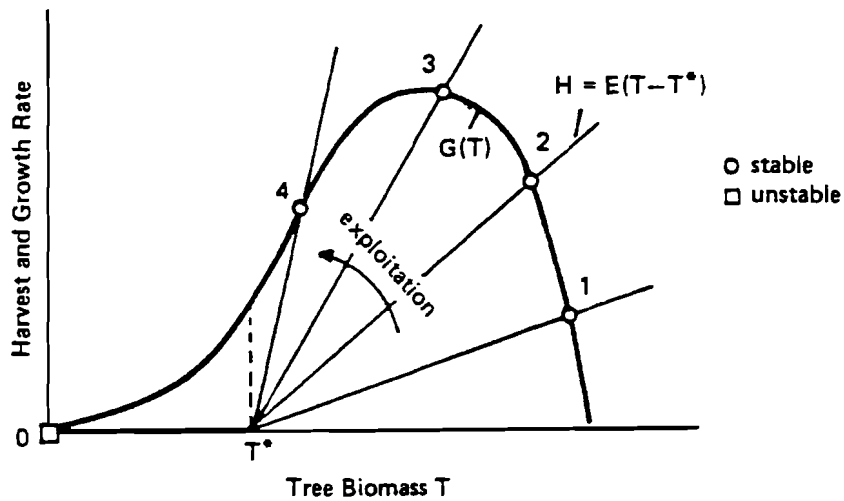


FIGURE 5. How catastrophes can be prevented when depensation is present.

As a second example, we now consider the case in which the harvesting function $h(T)$ is concave (second type functional response). This is in practice the problem considered by Noy-Meir (1975) with grazed vegetation substituted by trees and herbivores substituted by man. Since we have already shown that depensation can give rise to catastrophes, we assume that the natural growth rate is of standard compensatory type. Although it is not necessary we further consider, for the sake of simplicity, the case of *logistic growth* for tree biomass. Thus, the forest dynamics is given by

$$\frac{dT}{dt} = rT\left(1 - \frac{T}{K}\right) - \frac{ET}{\alpha + (c + p)T} \quad (6)$$

where K is the *carrying capacity* and r the *intrinsic rate of increase*. The equilibria can be found by intersecting the curves $H = E h(T)$, corresponding to the particular harvesting function (5), with the logistic

parabola $G(T)$ (see Figure 6). For a particular value E' of the exploitation ($E' = r\alpha$) the two curves $G(T)$ and $Eh(T)$ have the same tangent at the origin, as shown in Figure 6. By comparing the curvatures of these two curves at the origin (i.e., the second derivatives of the functions $G(T)$ and $Eh(T)$) it is easy to prove that if $\alpha/K > c + p$ there are no multiple stable equilibria and hence no catastrophes; but if

$$\alpha/K < c + p \tag{7}$$

the outcome is as shown in Figure 6. Since this figure is structurally equivalent to Figure 3, we can conclude that when Eq. (7) is satisfied a reversible catastrophe takes place and tree biomass and harvest rate vary with exploitation as shown in Figure 4.

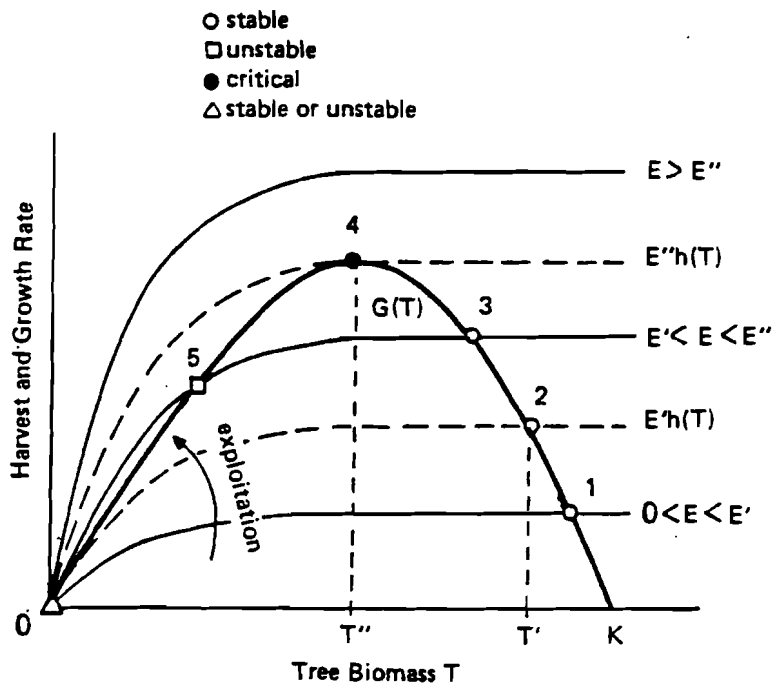


FIGURE 6. Concave harvesting policies $Eh(T)$ and multiple equilibria.

Notice that α/K is the time for the search of a unit biomass when the unexploited forest is at its carrying capacity. Therefore, the condition for the occurrence of a collapse (Eq. (7)) is that the time for cutting and transporting a unit biomass is greater than the time for searching it, a condition which is obviously very often satisfied in practice.

5. SOIL NUTRIENT AND CATASTROPHES

In this section we account for the dynamics of the nutrient in the forest and we show that, under suitable circumstances, the interactions between tree biomass and nutrients can give rise to catastrophes.

The Model

Since we have already shown that the concavity of the harvesting function can be *per se* the cause of catastrophes, in order to stress the role of the nutrient we now assume that the harvest H is linearly related to tree biomass (see Eq. (2)). The second basic assumption is that the nutrient pool for the trees can be described by the concentration N of one nutrient which is homogeneously distributed in the soil. This hypothesis is crude although it is well-known that usually only one element (most often nitrogen) limits productivity in forests (see, for instance, Cole & Rapp 1981, Ågren & Kauppi 1983, Vitousek & Matson 1984).

The model is as follows

$$\frac{dN}{dt} = W - \alpha N - bNT + cm(N)T \quad (8a)$$

$$\frac{dT}{dt} = [ebN - dT - m(N) - E]T \quad (8b)$$

where a, b, c, d, e are positive parameters, E is the exploitation, W is the input to the nutrient pool from sources other than tree decomposition, and $m(N)$ is the tree mortality.

In Eq. (8a) the negative term $-aN$ represents both the leaching losses (which at least for nitrogen are proportional to the nutrient concentration in the soil, see Abrahamsen 1980) and the uptake by the remaining vegetation.

The second negative term $-bNT$ in Eq. (8a) is the nutrient uptake from the soil. The underlying assumption is that the root system is proportional to the above-ground biomass and that each root pumps up a constant amount of water per unit tree biomass so that the total uptake is proportional to T and N (*passive uptake*). This is, at least partially, unrealistic since a tree can develop, if needed, roots in a soil layer which is temporarily free from a too high nutrient concentration. However, when W and hence N are sufficiently high the nutrient reaches also those layers and our assumption becomes less crude.

If the amount of nutrient contained in each unit of standing biomass is roughly constant (as shown by Sprugel 1984 with reference to balsam fir), then the nutrient transferred back to the soil by decomposition is proportional, through a multiplicative coefficient c , to the dying tree biomass $m(N)T$. Here we make the strong assumption that decomposition is fast, since the flow of nutrient from the decomposable dead biomass enters the balance of the soil pool (Eq. (8a)) without any time delay. It should be noticed, however, that the components of the dead biomass which are most readily decomposed (foliage and branches) are usually richest in nutrient content (Sprugel 1984). For these

components mineralization is achieved with a time delay which is small when compared with tree lifetime.

In Eq. (8b) the term $ebN - dT$ represents the primary productivity. Therefore, the production of new biomass per unit biomass is enhanced by the nutrient uptake bN (the parameter e being an efficiency conversion factor), but inhibited when the total standing biomass is too high. This density dependence stands for root competition and increased shading, which limits the amount of energy captured from the surrounding environment by each tree unit (see Silvertown 1982).

The final and perhaps most important comment on the model is deserved by tree mortality m . If there were no adverse effects of acidic deposition only natural mortality would be present and m might be presumed constant. However, if the nutrient inflow W is partly represented by acidic precipitation there might be several direct and indirect mechanisms for increased tree mortality. One of them, that we like to consider here, is due to the increase in *soil acidity*. As it is well-known, there are several buffering reactions in the forest soils which can partially counteract the effect of acidic deposition (Matzner & Ulrich 1981), but when *pH* falls below 5 the solubility of *aluminum* increases sharply and if *pH* is less than 4.2, which occurs in many forest soils of Central Europe, the aluminum buffer range is reached: aluminum ions are present in high concentrations and can be toxic to bacteria and plant roots. Contemporarily the leaching of *calcium*, *magnesium*, and possibly *potassium*, which are vital, though usually non-limiting factors, is enhanced. With even lower *pH* values most heavy metals are mobilized and can damage the trees. As soil acidity is positively correlated with

nutrient concentration in the soil, the assumption that follows is that mortality is a function of N . Such a function $m(N)$ is constant up to a certain value and thereafter very sharply increasing.

Before analyzing the stability of the equilibria of model (8) we like to stress that none of the properties pointed out in the following strictly rely upon the particular analytical form chosen to describe the various phenomena. For example, one could assume that primary productivity is increasing with N in a nonlinear way, or take inhibition in tree growth into account by making the efficiency e decreasing with respect to T , and only the analytics would change but not the results. In other words, although the model is quite particular we argue that the basic features it points out are generic.

Analysis of the Equilibria

The equilibria (\bar{N}, \bar{T}) can easily be found by annihilating the two derivatives dN/dt and dT/dt in Eq. (8). Geometrically, the equilibria can be visualized in the state space (N, T) as the intersections of the two *isoclines*, which are Eq. (8a) with $dN/dt = 0$ and Eq. (8b) with $dT/dt = 0$, respectively. Thus, the first isocline is given by

$$T = \frac{1}{c} \frac{W - aN}{\frac{b}{c}N - m(N)} \quad (9a)$$

while the second one is given by

$$T = 0 \quad T = \frac{1}{d} [ebn - m(N) - E] \quad (9b)$$

The isoclines (9a) can be parametrized with respect to the nutrient inflow W , while the isoclines (9b) depend upon the exploitation E . In

Figure 7 we show how these isoclines can be found starting from the mortality function $m(N)$ and how they vary with W and E , respectively.

Once W and E are fixed at two prescribed values, we can have one or more intersections of the isoclines. In Figure 8, for example, we have a case with two equilibria: point 1 corresponds to tree extinction in the forest, while point 2 represents a viable forest. The stability analysis of these equilibria is very simple and can be carried out via *linearization*.

For example, the *Jacobian matrix* of the system

$$J = \begin{bmatrix} -a - [b - cm'(N)]T & -bN + cm(N) \\ [eb - m'(N)]T & [ebN - dT - m(N) - E] - dT \end{bmatrix}$$

at point 1 ($T = 0, N \neq 0$) is given by

$$J = \begin{bmatrix} -a & -bN + cm(N) \\ 0 & ebN - m(N) - E \end{bmatrix}$$

Since J is in triangular form, its diagonal elements are the *eigenvalues*. The first one ($-a$) is negative while the second ($ebN - m(N) - E$) is positive (see Figure 8b), thus implying that point 1 is an unstable equilibrium point (a *saddle point*). A similar, though more tedious, analysis of the Jacobian matrix allows the conclusion that point 2 in Figure 8 is stable.

Catastrophes

We can now focus on the problem we like to discuss in this paper, namely the possibility of catastrophes in forest ecosystems.

If we consider the exploitation E as a slowly varying parameter we can have five different cases depending upon the value of the nutrient inflow W . This is summarized in Figure 9 which must be read column by column starting from the left side. In case (i) when $W < aN_{10}$ there is

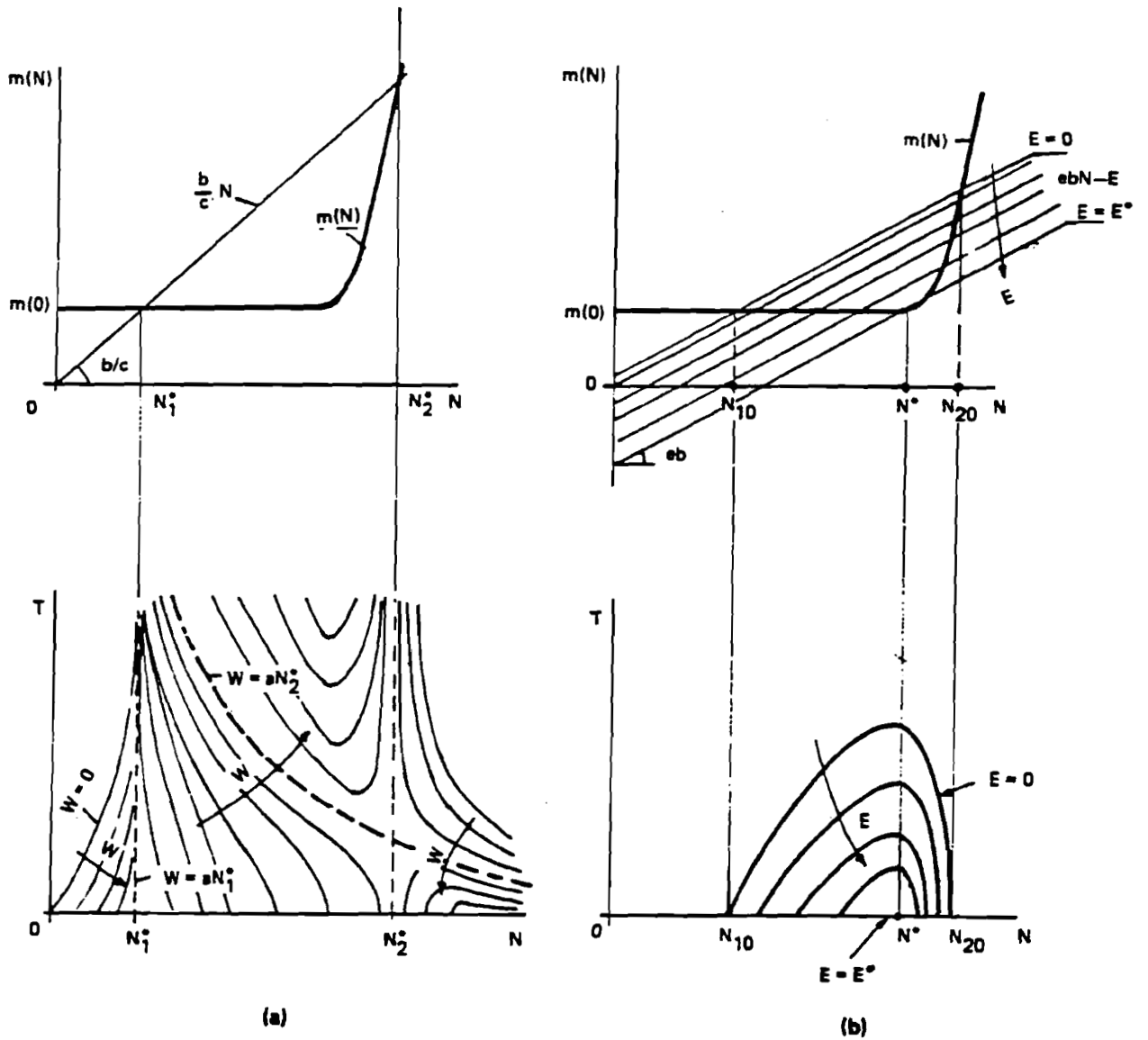


FIGURE 7. (a) The isoclines $dN/dt = 0$ when W is varied; (b) the isoclines $dT/dt = 0$ when E is varied.

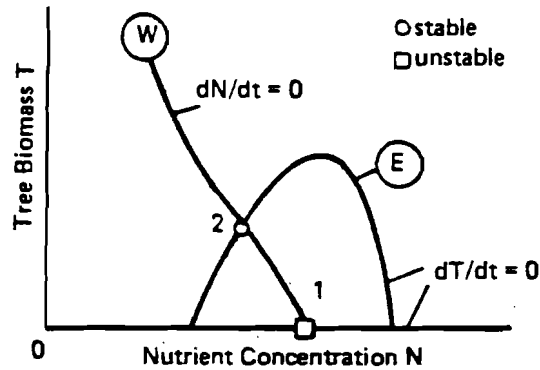


FIGURE 8. The equilibrium points 1 and 2 are found by intersecting the isoclines.

only one stable equilibrium point, namely the extinction of the trees, and this is obviously true for all values of E . A similar situation occurs in case (v) which is characterized by very high values of W , namely $W > \alpha N^{**}$. This means that the trees cannot survive if the nutrient inflow into the system is either too low or too high. On the contrary, trees can exist in the three other cases, i.e., when

$$\alpha N_{10} < W < \alpha N^{**}$$

provided the exploitation is not too high. In case (ii) the stable non-trivial equilibrium is characterized by a smooth decline to zero of tree biomass. Therefore, in this case, there is no catastrophe when the exploitation is slowly increased. On the contrary, in case (iii) we have a catastrophe since trees collapse for $E > E''$. Nevertheless, this catastrophe is reversible since a bloom takes place if the exploitation is lowered below the critical value E' . Finally, in case (iv) the catastrophe

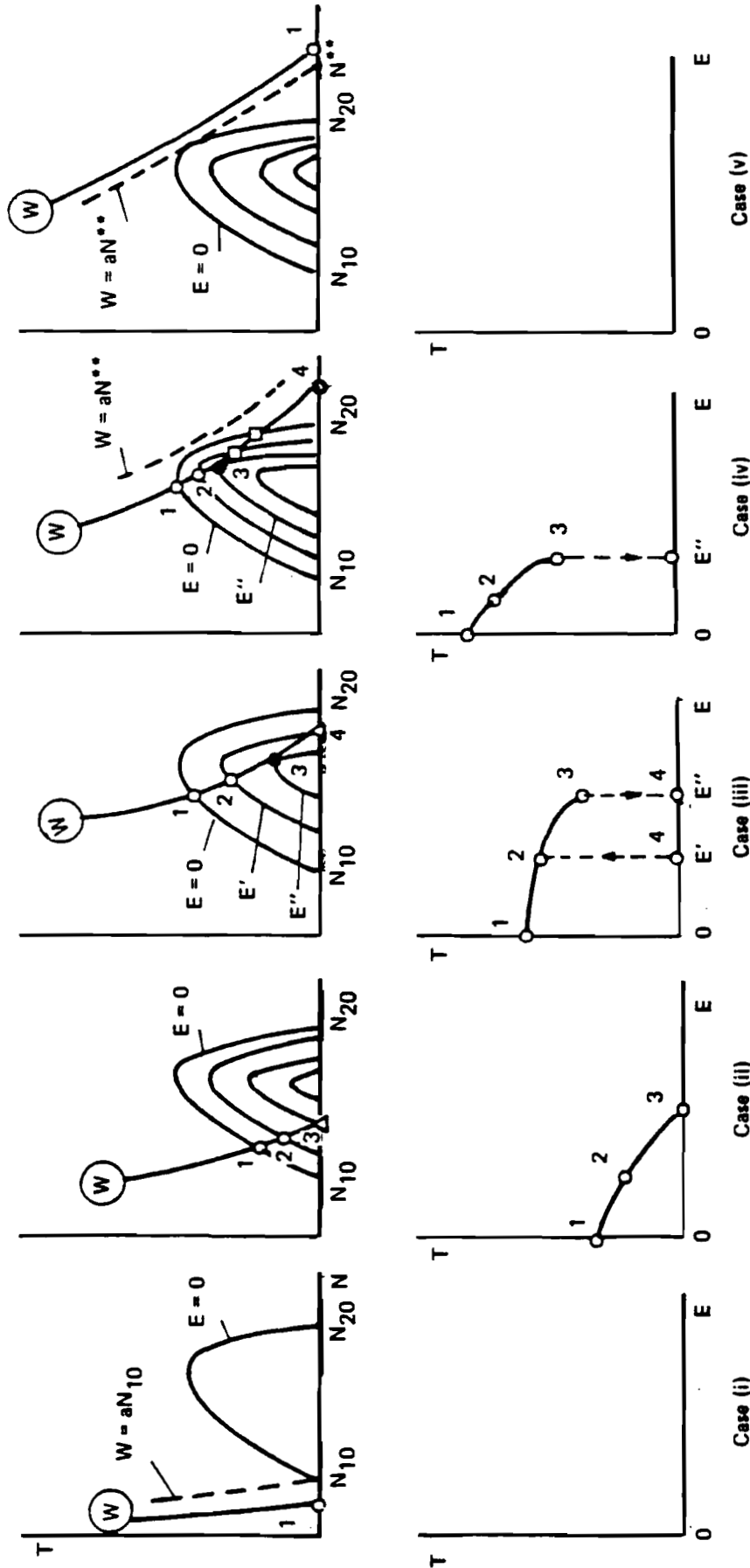


FIGURE 9. The figure shows (column by column) the five different modes of behavior. Case (i): tree extinction is the only stable equilibrium; Case (ii): trees can survive but smoothly decline to zero when exploitation is increased; Case (iii): reversible fold catastrophe; Case (iv): irreversible fold catastrophe; Case (v): tree extinction is the only stable equilibrium.

is irreversible since the nutrient inflow W is so high that the extinction is always a stable equilibrium point. All this can be simply summarized by saying that the chances of a collapse of the trees in the forest due to overexploitation are enhanced by the nutrient inflow into the soil.

A similar analysis can be done by considering W as a slowly varying parameter and fixing the exploitation E at a given value. Figure 10 shows the result, namely a reversible fold catastrophe. This proves that exploited natural forests are potentially exposed to catastrophic collapses if acidic deposition becomes heavier and heavier.

The results of the overall analysis can be summed up by defining in the space of the two parameters E and W all the regions corresponding to different modes of forest behavior. These regions are shown in Figure 11 where the two solid lines represent the potential catastrophes: the highest one corresponds to a collapse of the trees when it is crossed from below (increase of acidic deposition) or from the left (increase of exploitation), while the lowest one corresponds to a bloom of the trees when it is crossed from above or from the right. The two lines form a cusp at point (E^*, aN^*) and for this reason this type of catastrophe has been named *cusp catastrophe*. The figure shows that for any given nutrient inflow W there is an upper limit to the exploitation E , above which the trees cannot survive. In particular if

$$aN_{10} \leq W \leq aN^*$$

tree biomass tends to zero when the exploitation approaches its upper limit, while if

$$aN^* < W < aN^{**}$$

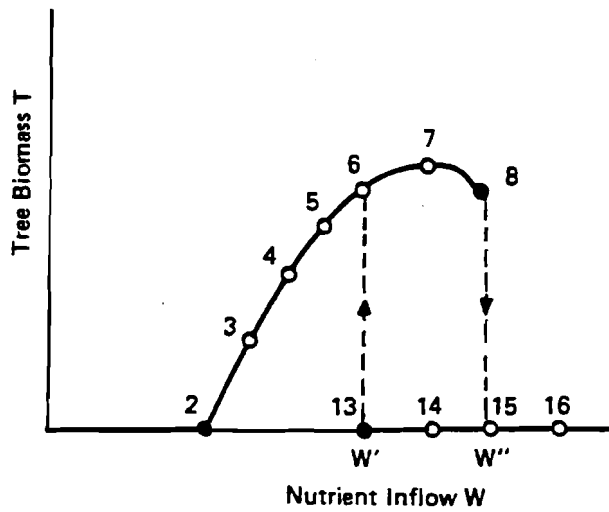
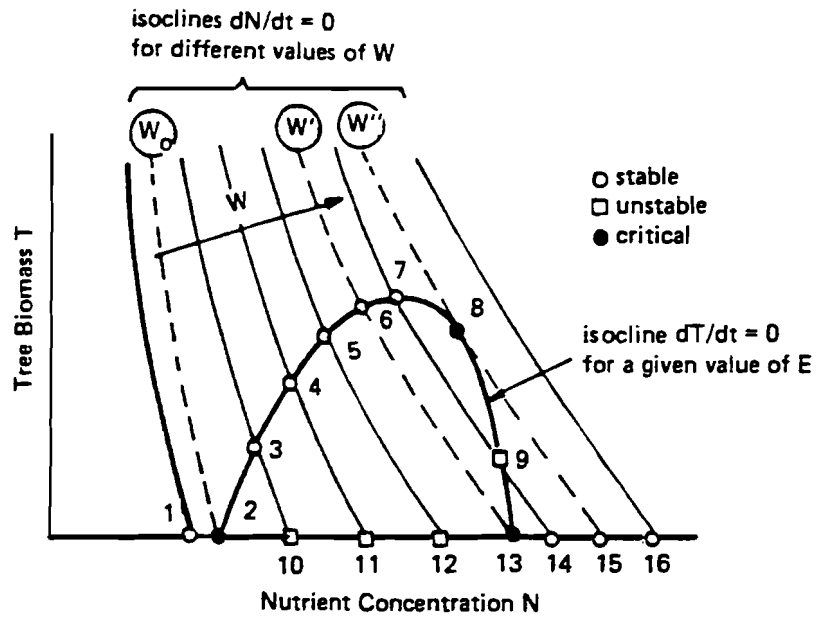


FIGURE 10. (a) The equilibria in the state space for different values of W ; (b) tree biomass T vs. nutrient inflow W ; the points W' and W'' mark the catastrophes.

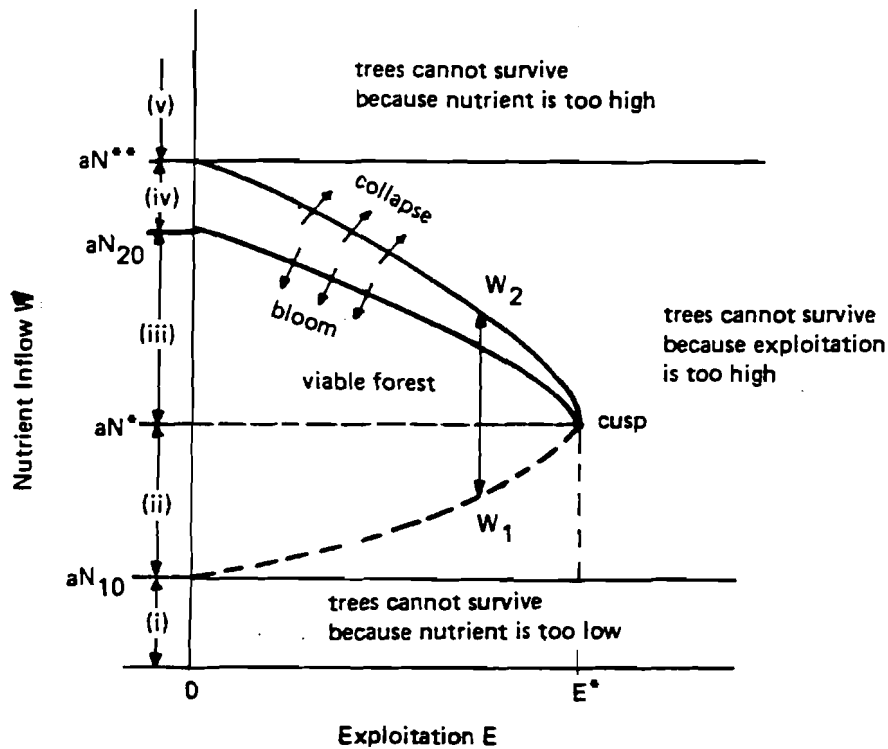


FIGURE 11. The cusp catastrophe and the regions with different modes of behavior. The partition (i),(ii),..., (v) of the vertical axis makes reference to the classification of Figure 9.

a catastrophic collapse of the trees is obtained if this upper limit is exceeded. Conversely, if the exploitation E is smaller than the limit value E^* there exists an interval $[W_1, W_2]$ of nutrient inflows for which the forest is viable (see Figure 11). This interval nevertheless becomes smaller and smaller when the exploitation is increased. In conclusion, we can say that human exploitation and acidic deposition have a kind of negative synergistic effect.

6. CONCLUDING REMARKS

In this paper we have shown that overexploitation of natural forests can give rise to catastrophic and possibly unexpected collapses of trees. The basic mechanisms for this are many and quite diversified. Among them we have depensation in the growth curve and concavity of the harvesting function. But more interesting is the catastrophe which is proved to exist when tree mortality strongly increases with soil acidity. This case has been analyzed in detail in the paper and the main conclusion is that the catastrophe is a "cusp" with respect to exploitation and acidic deposition. This means that a collapse of the trees in the forest can arise when exploitation and/or acidic deposition are increased. Moreover, it is shown that the range of acidic deposition giving rise to a viable forest shrinks down to zero when exploitation is increased and that the limit to exploitation becomes smaller and smaller when acidic deposition is increased. All these qualitative properties, which have been formally proved, might represent one of the possible ways of interpreting some of the numerous forest collapses which have been recently reported in the literature.

Investigations of other mechanisms which might generate catastrophes in exploited or unexploited forests should be possible following the guidelines outlined in the paper. Among them we certainly have a number of important and interesting mechanisms for increased tree mortality (like damage to foliage or uptake of toxic substances) which are directly or indirectly related to the increase of acidic precipitation.

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