Some models of catastrophic behavior in exploited forests

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Abstract

This paper presents some models which show that small variations of the human exploitation of a natural forest can give rise to dramatic changes in the forest biomass. Two simple mechanisms for catastrophes, already pointed out for other ecosystems, are briefly discussed at the beginning of the paper. A more interesting mechanism for catastrophes is then presented. It is based on a model of the dynamics of forest biomass and soil nutrients and on the fact that mortality may become very high when soil acidity exceeds a threshold. 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, which brings about also acidic deposition, is sufficiently high. Moreover, such a catastrophe is irreversible, i.e., regeneration is not possible, if the nutrient inflow is too high.

Introduction

Both theory and observation indicate that some ecosystems are likely to possess several different equilibrium points (see May, 1977). This implies that substantial natural disturbances (such as, for example, wind, fire, pest, or release of toxic substances in the case of a forest) may perturb an ecosystem from a stable equilibrium into the region of attraction of another stable equilibrium. Thus, in these cases, the state of the system 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 below).

In this paper we outline three mechanisms which cause catastrophes in the dynamics of models 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 forest 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 soil nutrients. 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 may depend upon the exogenous inflow of nutrient due to natural sources, fertilization and acidic deposition, also the possibility of collapse and regeneration may depend upon this inflow.

The mathematical models we use are very crude. We take in fact a short-cut approach to the problem by lumping many different phenomena into a single

equation of biomass 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 (see Shugart, 1984, for a review).

On catastrophes

Catastrophe theory (see Thom, 1972; Zeeman, 1977) has started to be used in ecology (e.g., Jones, 1977; Bazin & Saunders, 1978; Casti, 1982: Kempf *et al.,* 1984). It can be introduced as follows.

A basic ingredient is a measure E of forest exploitation, which can be quantified in various ways, for instance, the percentage of mature trees that can be cut per year, or the amount of labor and capital employed in felling trees.

If exploitation is kept constant over time, the state of the system, i.e., the variables that fully characterize the ecosystem (tree standing biomass, harvested biomass, nutrient concentration, etc.) will converge, in the absence of natural disturbance, to one of its possibly many stable equilibria. When exploitation is smoothly and slowly increased also these equilibria will vary smoothly. But sometimes a small (infinitesimal) perturbation of the exploitation E from a particular given value $\bar{E}$ entails disappearance of the equilibrium. In other cases, the equilibrium which is stable for $E < \bar{E}$ becomes critical for $E = \bar{E}$ and unstable for $E > \bar{E}$. 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. Often there are two critical values of the exploitation: a typical situation is as in Fig. 4 which refers to a model detailed later on. The solid curves describe the values of forest biomass at equilibrium for different exploitations: notice that in between

the critical values E' and E'' there are two stable equilibria, one of which is extinction. If exploitation is slowly increased from zero, biomass T smoothly declines (see open circles 1, 2, 3) until the critical value E'' is reached (closed circle 4) where a catastrophic transition from T'' to extinction occurs because for bigger exploitation pressure only the null biomass is a stable equilibrium. After this collapse, decreasing the exploitation will have no effect (the state of the ecosystem is 'trapped' in the extinction equilibrium) until the critical value E' is reached where biomass can regrow to the level T'. If E' is zero the catastrophe is called *irreversible* for obvious reasons, *reversible* otherwise.

Growth and harvesting functions

We consider a forest, not at the level of a single stand, but as a mosaic tessellated with many small patches. In this case it is not unrealistic to assume that the biomass response of the forest landscape can be described by a single differential equation (see Shugart, 1984, pp. 134–138).

Let $T(t)$ be the total standing biomass in the forest at time t. Then, if the forest is not exploited, the rate of change dT/dt of biomass is simply the natural growth rate G which is here assumed to be a function of forest biomass only. In the normal compensatory case the growth rate per unit biomass $G(T)/T$ is a decreasing function of total biomass (density-dependence operates via increased mortality and/or decreased fertility) and $G(T)$ is concave as shown in Fig. 1. Sometimes, however,
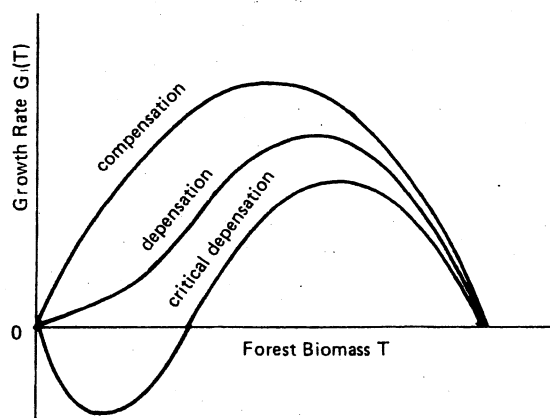

Fig. 1. Different types of natural growth rate functions.

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 & Schubert, 1956) and by Abert squirrels (Larson & Schubert, 1970) is an increasing function of crop size. Also, other mechanisms come to mind like resistance to wind throw and moisture retaining capacity in the soil. 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 Fig. 1.

When the forest is exploited, the rate of change dT/dt of standing crop is the difference between natural growth rate G and harvesting rate H. In real world situations 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 biomass only, i.e., $H=H(T)$. This function will be called *harvesting policy* in the following. Moreover, let us write

$$H(T)=E\,h(T) \tag{1}$$

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 due to variations of the harvesting function $h(T)$ or to variations of the exploitation E, the object of this paper.

There are several possible shapes for the harvesting function $h(T)$. The simplest is related to the use of *percent quotas*, which means that a fixed percentage of the standing trees can be felled each year. In this case the harvesting policy is simply given by

$$H=ET \tag{2}$$

where the exploitation E is proportional to the percentage of standing biomass that can be harvested each year (Fig. 2, curve a).

A second shape for $h(T)$ follows from the assumption that E represents, in suitable units, the amount of labor and capital invested. Then the harvesting rate cannot indefinitely increase with biomass, because, given E, a certain finite harvesting capacity cannot be exceeded. Thus the harvesting function must be a saturating one. A possible analytical choice (see Holling, 1959) is

$$H=Eh=ET/(\alpha+\beta T) \tag{3}$$

with α and β positive parameters (Fig. 2, curve b).

Finally, if one considers that lumbering may not be rewarding when the forest biomass is low (e.g., because this biomass mostly consists of young, nonmarketable trees), a third possible shape for the harvesting function is a sigmoid one (Fig. 2, curve c).

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.,

$$dT/dt=G(T)-ET$$

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 Fig. 3).
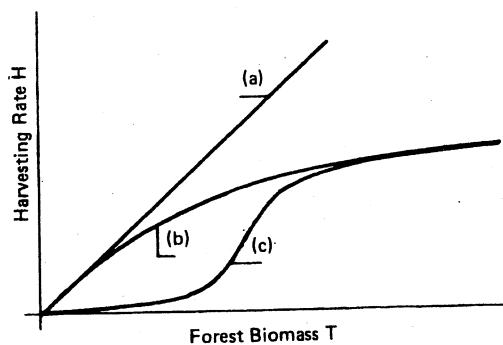

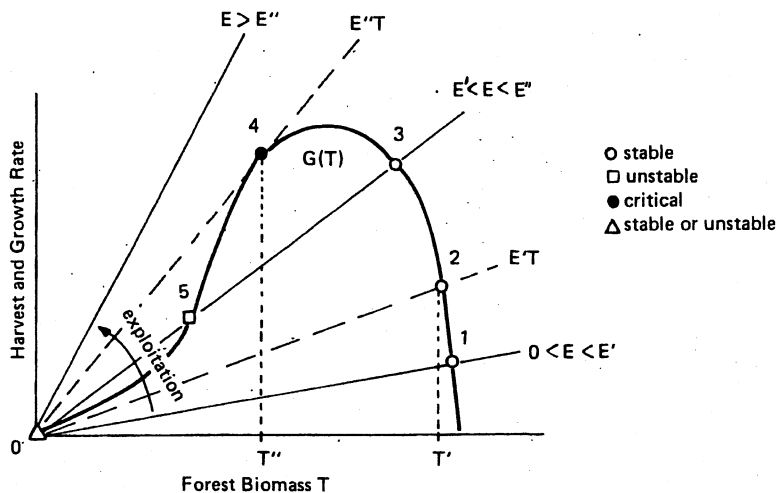*Fig. 2.* Different types of harvesting policies: (a) *linear* (percent quotas), (b) *concave*, (c) *sigmoid.*

Fig. 3. Depensation in the growth rate *G(T)* and multiple equilibria.

If the exploitation is low, i.e., $0<E<E'$, where at the origin (see Fig. 3), there are two equilibria: the extinction (point 0) which is *unstable* and a nontrivial steady state (point 1) which is *stable*. For higher exploitation, i.e., when $E'<E<E''$ where E'' is defined in Fig. 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 biomass T and of the harvest rate H versus exploitation are as shown in Fig. 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 standing crop smoothly decreases (see points 1, 2, 3, 4 along the growth curve of Fig. 3) until the critical value T'' is reached (see Fig. 4). At that point if the exploitation is further increased, trees die and the forest collapses (recall that point 0 of Fig. 3 is stable for $E>E''$). Now, if the exploitation E is reduced after the new equilibrium $T=0$ has been reached or approached, trees do not grow any more unless ex-
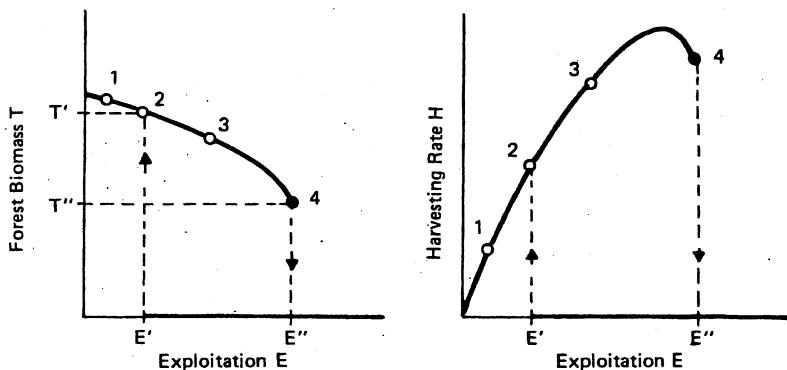

Fig. 4. Standing crop T and harvesting rate H vs. exploitation E when depensation is present. The values E' and E'' of the exploitation mark the critical values of the fold catastrophes. The points 1, 2, 3 and 4 are the same as in Fig. 3.

ploitation is substantially decreased. In fact, only when E becomes smaller than the critical value E'', point 0 in Fig. 3 becomes unstable again and the tree biomass sharply increases toward the value T'' (see Fig. 4). This type of catastrophe, which essentially points out the existence of a *hysteresis*, is called *fold catastrophe*.

When depensation 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 regeneration is not possible once the critical exploitation E'' has been exceeded.

As a second example we now consider the case in which the harvesting funtion $h(T)$ is concave. This is in practice the problem considered by Noy-Meir (1975) with grazed vegetation replaced by trees and herbivores 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

$$\frac{dT}{dt} = rT(1 - \frac{T}{K}) - \frac{ET}{\alpha + \beta T} \tag{4}$$

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 Fig. 5). For a particular value E' of the exploitation ($E' = r\alpha$) the two curves $G(T)$ and $E\ h(T)$ have the same tangent at the origin, as shown in Fig. 5. 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 $\alpha/K > \beta$ there are no multiple stable equilibria and hence no catastrophes; buf if

$$\alpha/K < \beta \tag{5}$$

the outcome is as shown in Fig. 5. Since this figure is structurally equivalent to Fig. 3, we can conclude that when Eq. (5) is satisfied a reversible catastrophe takes place and forest biomass and harvest rate vary with exploitation as shown in Fig. 4.
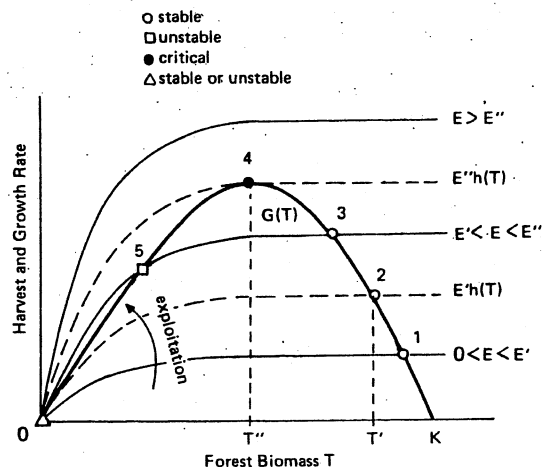

Fig. 5. Concave harvesting policies $E\ h(T)$ and multiple equilibria.

Soil nutrients and catastrophes

In this section we account for the dynamics of nutrients in the forest and we show that, under suitable circumstances, the interactions between standing crop, nutrients, and acid precipitation 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 nutrients we now assume that the harvest H is linearly related to forest biomass (see Eq. (2)). The second basic assumption is that the nutrient pool for the standing biomass 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

$$dN/dt = W - aN - bNT + cm(N)T \tag{6a}$$

$$dT/dt = [ebN - dT - m(N) - E]T \tag{6b}$$

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 decomposition, and $m(N)$ is the mortality. In Eq. (6a) the negative term $-aN$ represents the leaching losses, which at least for nitrogen are proportional to the nutrient concentration in the soil.

The second negative term $-bNT$ in Eq. (6a) 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 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 forest 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. (6a)) 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. If, on the contrary, time scales were comparable, one should introduce a more sophisticated model with a distinction between organic and inorganic nutrient pools. The dying tree biomass would be an input to the organic pool, which would slowly release a flow of inorganic nutrient to the other pool.

In Eq. (6b) 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, which allows us to take acidic deposition into account. As is well known, one of the most important mechanisms for increased tree mortality is believed to be abnormal soil acidity (Matzner & Ulrich, 1981), because when pH falls below 5 aluminium solubility sharply increases. Owing to air pollution, precipitation is both carrying nutrient (e.g., nitrogen compounds) and acidity. Therefore increased emissions imply a bigger nutrient inflow W to the soil but also a greater acidic input. It follows that increasing N concentration is very often paralleled by increasing soil acidity. All this supports the assumption that mortality is a function of N, which is roughly constant up to a certain value and thereafter very sharply increasing.

It should be clear that the results which follow from the analysis of this model are direct consequences of the specific combination of phenomena we have taken into consideration. There is a whole array of other mechanisms, in particular due to acidic precipitation, which influence the growth and mortality of trees. Certainly, all of them play a role in a forest dynamics. Therefore, the link between the formal conclusions that will follow and the reality of a forest may be rather weak, unless the phenomena represented in our model are dominant, so that the real forest behaves at least qualitatively like our hypothetical (6).

Analysis of equilibria

The equilibria $(\bar{N}, \bar{T})$ can easily be found by annihilating the two derivatives dN/dt and dT/dt in Eq. (6). Geometrically, the equilibria can be visualized in the state space (N, T) as the intersections of the two *isoclines*, which are Eq. (6a) with $dN/dt = 0$ and Eq. (6b) with $dT/dt = 0$, respectively. Thus, the first isocline is given by

$$T = \frac{1}{c} \frac{W - aN}{\frac{b}{c}N - m(N)} \tag{7a}$$

while the second one is given by

$$T = 0 \qquad T = \frac{1}{d}[ebn - m(N) - E] \tag{7b}$$

The isoclines (7a) can be parametrized with respect to the nutrient inflow W, while the isoclines (7b) depend upon the exploitation E. In Fig. 6 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 Fig. 7, 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*, but is not detailed here.

Catastrophes in forest ecosystems

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
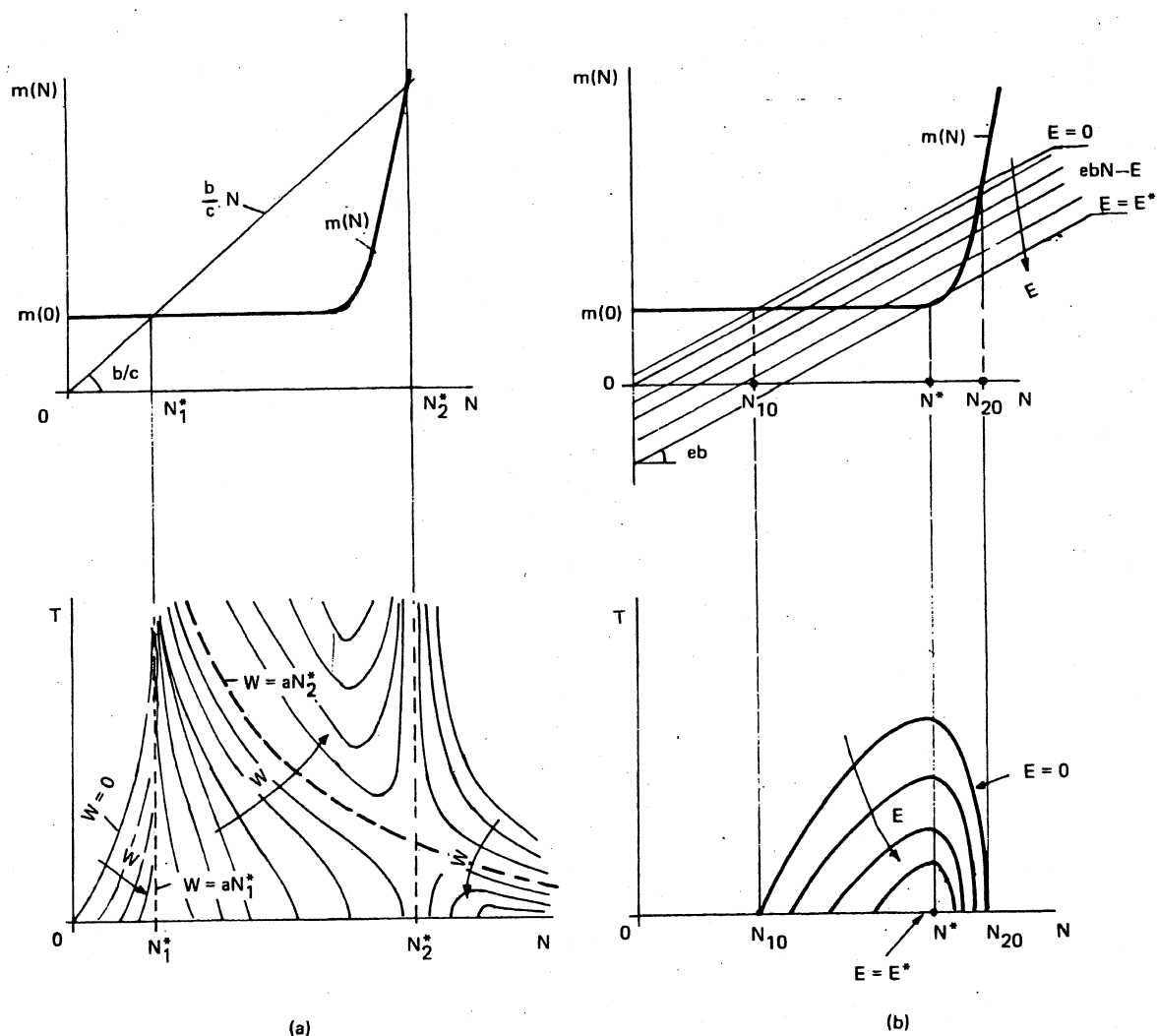

Fig. 6. (a) The isoclines $dN/dt = 0$ when W is varied; (b) the isoclines $dT/dt = 0$ when E is varied.
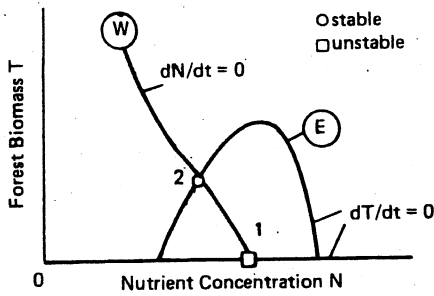
Fig. 7. The equilibrium points 1 and 2 as found by intersecting the isoclines.

Fig. 8 which must be read column by column starting from the left side. In case (i) when $W < aN_{10}$ there is only one stable equilibrium point, namely the forest extinction, 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 $W > aN^{**}$. This means that our hypothetical forest cannot survive if the nutrient inflow to the system is either too low or too high. On the contrary, the forest is viable in the three other cases, i.e., when $aN_{10} < W < aN^{**}$ provided the exploitation is not too high. In case (ii) the stable non-

trivial equilibrium is characterized by a smooth decline to zero of forest 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 the forest collapses for $E > E''$. Nevertheless, this catastrophe is reversible as regeneration takes place if the exploitation is lowered below the critical value E'. Finally, in case (iv) the catastrophe is irreversible since the nutrient inflow W is so high that extinction is always a stable equilibrium point. All this can be simply summarized by saying that the chances of a forest collapse due to overexploitation are enhanced by high nutrient (hence acidity) inflow into the soil.

A similar analysis can be done by considering W as a slowly varying parameter and fixing the exploitation E at given value. Fig. 9 shows the result, namely a reversible fold catastrophe. This may be taken as a demonstration 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 all the regions corresponding to different modes of behavior in the space of the two parameters E and W. These regions are shown in
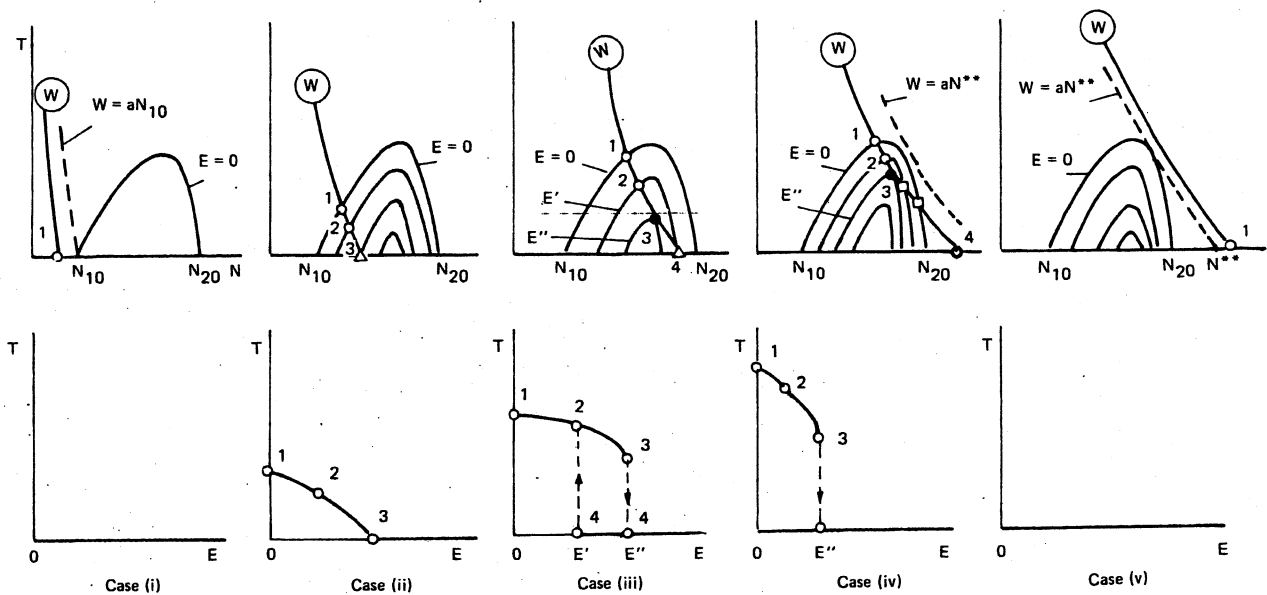

Fig. 8. The five different modes of behavior. (i): forest extinction is the only stable equilibrium; (ii): forest can survive but biomass smoothly declines to zero when exploitation is increased; (iii): reversible fold catastrophe: (iv): irreversible fold catastrophe; (v): forest extinction is the only stable equilibrium.
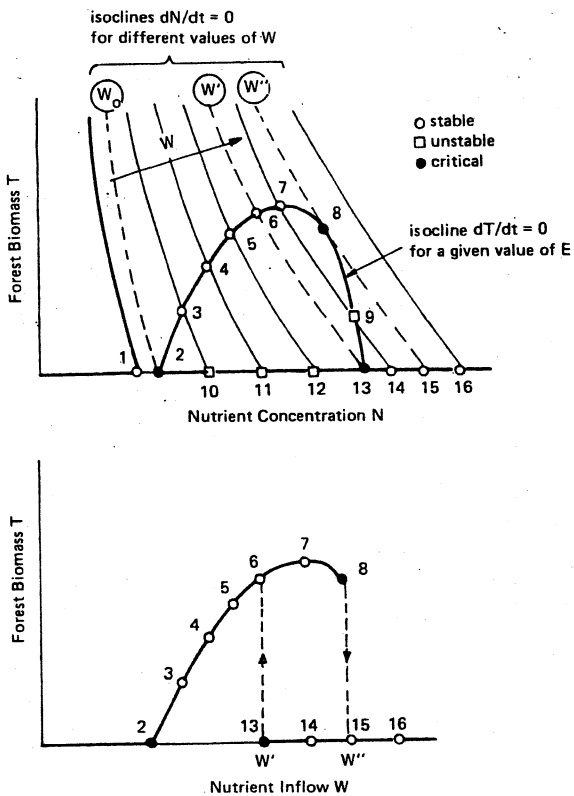
Fig. 9. (a) The equilibria in the state space for different values of W; (b) biomass T vs. nutrient inflow W: the points W' and W'' mark the catastrophes.

Fig. 10 where the two solid lines represent the potential catastrophes: the highest one corresponds to a collapse when it is crossed from below (increase of acidic deposition) or from the left (increase of exploitation), while the lowest one corresponds to forest regeneration 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 our hypothetical forest is doomed to extinction. In particular if $aN_{10} \le W \le aN^*$ the biomass tends to zero when the exploitation approaches its upper limit, while if $aN^* < W < aN^{**}$ a catastrophic collapse occurs 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 Fig. 10). This interval nevertheless becomes smaller and smaller when the exploitation is increased. In conclusion, it looks like human exploitation and acidic deposition have a kind of negative synergistic effect.
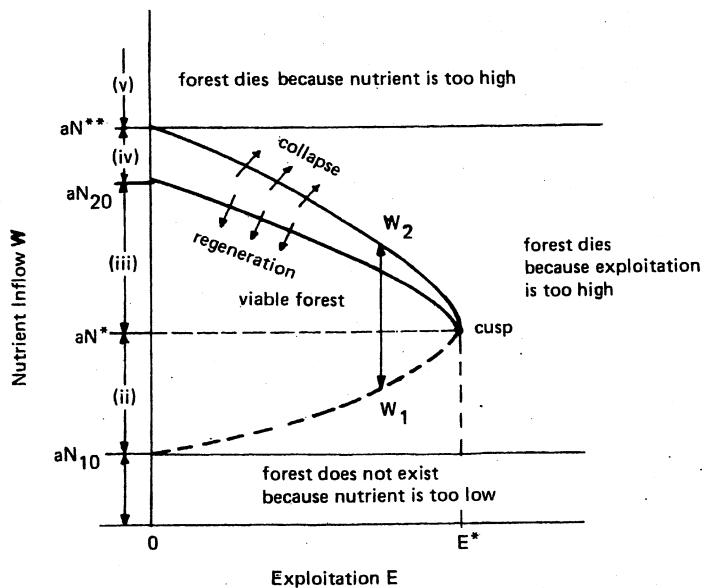

Fig. 10. The cusp catastrophe and the regions with different modes of behavior. The partition (i), (ii), ..., (v) of the vertical axis makes reference to the classification of Fig. 8.

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Concluding remarks

Our modeling exercise shows that overexploitation of a hypothetical natural forest can lead to catastrophic and possibly unexpected collapses. The basic mechanisms for this are many and quite diversified. Among them we have pointed to depensation in the growth curve and concavity of the harvesting function. But more interesting is the catastrophe which is predicted by a nutrient-biomass model when 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 in such a forest a collapse can occur when exploitation and/or acidic deposition are increased.

Investigations of other mechanisms which might generate catastrophes in exploited or unexploited forests should be possible developing similar modeling exercises. 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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