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Sahelian rangeland development; a catastrophe?

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Abstract

This paper sets out that the dynamics of the Sahelian rangeland vegetation can be interpreted as a cusp catastrophe and that this interpretation offers a promising basis for the description and analysis of this ecosystem.

Firstly, an existing scheme of the dynamics of Sahelian herbaceous vegetation is translated into the state-and-transition formulation. Secondly, the application of the cusp catastrophe is explored by studying the behaviour of the Sahelian rangeland ecosystem under changing effective rainfall and grazing intensity, using the transitions from the state-and-transition formulation as vectors along the cusp manifold. This conceptual cusp catastrophe model subsequently results in the identification of hypotheses and the detection of 5 catastrophic properties of this ecosystem (bimodality, inaccessibility, sudden jumps, divergence and hysteresis) that have important management implications.

The continuous and the discontinuous processes occurring in the Sahelian rangeland ecosystem can both be captured in a unified conceptual model by applying the cusp catastrophe theory. Testing the hypotheses generated by the conceptual model and searching for additional catastrophic properties, such as divergence of linear response and critical slowing down, is a useful direction for future research.

Key Words: catastrophe theory, discontinuous processes, Sahelian rangelands, vegetation dynamics.

The classical application of predator-prey graphs to plant-herbivore systems by Noy-Meir (1975) showed that simple grazing systems may be characterized by discontinuous stability. This suggested that catastrophe theory (Thom 1975, Zeeman 1976, Saunders 1980, Gilmore 1981) might be useful for describing system behaviour. Loehle (1985) developed this idea and created an analytical model for describing equilibrium states for simple grazing systems by recasting the general relationships presented by Noy Meir (1975) as a cusp catastrophe. Loehle (1985) also suggested that system behaviour be analysed by using a vector along the cusp manifold, under fluctuating rainfall and grazing intensity. However, he gave no concrete examples in his paper. Jameson (1988) presented an example applied to a mixture of cool season (C3) and warm season (C4) rangeland plants. However, the analysis of that example remained rather cursory and therefore Jameson's work merely indicates the potential applicability of the cusp catastrophe to modelling rangeland ecosystem dynamics (Lockwood and Lockwood 1993).

Lockwood and Lockwood (1993) pointed out that catastrophe theory has the potential of creating a unified paradigm for rangeland ecosystem dynamics. They based their analysis on the existence of succession-based concepts and of state-and-transition concepts (Westoby et al. 1989) in rangeland ecology and management. Further, they showed that rangelands in general exhibit the 5 essential catastrophe flags: bimodality, inaccessibility, sudden jumps, divergence and hysteresis (Gilmore 1981). These catastrophe flags are illustrated in Fig. 1 as a brief reminder of the phenomena exhibited by the cusp catastrophe (see **Appendix** for the mathematical geometry of the potential functions and the bifurcation set that together determine the cusp catastrophe manifold).

The aim of this paper is to show that the Sahelian rangeland vegetation dynamics can be interpreted as a cusp catastrophe and that this concrete example of earlier ideas and speculation offers an interesting framework on which description and analysis of this rangeland ecosystem can be based. The aim is to expose verifiable hypotheses, rather than to produce a complete and perfect framework.

The Sahel

The African Sahel is the vegetation transition zone between the Sahara desert and the Sudanian savannas. The annual rainfall varies from 100 to 600 mm per year, and is associated with characteristic Sahelian plant species and communities. The vegetation consists primarily of grassland and open *Acacia* scrub (0 to 20% coverage) (Breman and De Wit 1983, Le Houérou 1989).

The main forces driving Sahelian rangeland dynamics are rainfall and grazing. The latter is the principal land use type in the Sahelian rangelands (Breman and Cissé 1977, Sinclair and Fryxell 1985). Bush fires play a minor role in the dynamics of semi-arid rangelands (Walker et al. 1981). Because the biomass is small and heterogeneous north of the 400 mm isohyet, fire is negligible here. South of this isohyet, the fires are mainly restricted to sandy areas (Breman et al. 1980).

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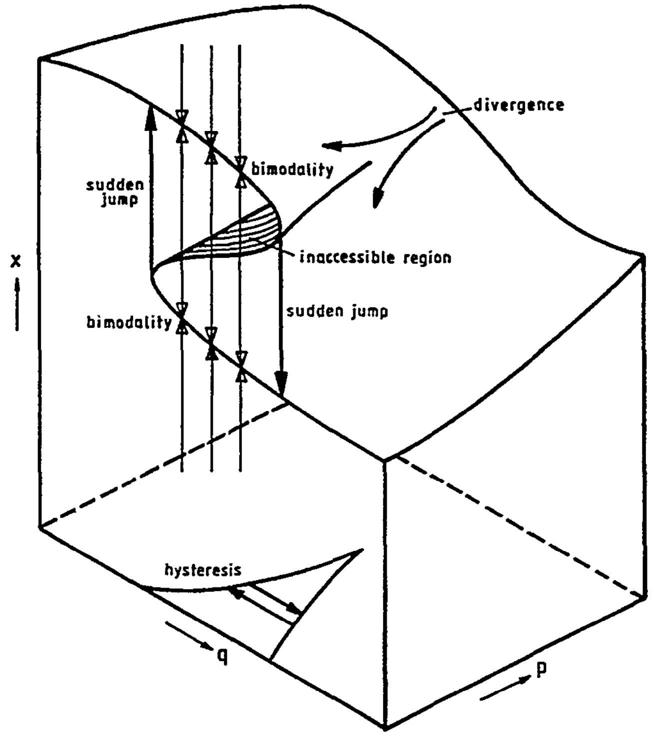

Fig. 1. The cusp catastrophe manifold with 5 catastrophe flags (Gilmore 1981, Lockwood and Lockwood 1993). These flags occur if the values of the control variables are within the bifurcation set, indicated by the cusp-shaped line on the horizontal control surface. The state variable is represented by x. The control variables are represented by p and q. See section Catastrophe flags for further explanation.

The geographical limits based on isohyets of mean annual rainfall should not be interpreted strictly. Rainfall is extremely variable from year to year (Tucker et al. 1991). Further, the vegetation of some areas with a mean annual rainfall higher than 600 mm, but with large differences between mean annual rainfall and effective rainfall which is the part that actually infiltrates the soil, can also be characterized as Sahelian (Breman and Stroosnijder 1982). As an example, on sandy soils the runoff rate may remain below 5%, but may exceed 50% on bare medium- to fine- textured soils with a sealed surface (Hoogmoed and Stroosnijder 1984, Le Houérou 1989, Casenave and Valentin 1992).

Human and livestock populations in the Sahel both increased by a factor of about 2.3 between 1950 and 1983 (FAO production yearbooks, cited by Le Houérou [1989]). This period included a drought of unprecedented duration lasting from 1970 to 1984 according to Le Houérou (1989). In these years the mean annual rainfall was about 60% of the 1900–1969 period. Tucker et al. (1991) discerned a period of wet years from 1950 to 1968 followed by dry years from 1969 to 1987.

The combination of increasing grazing intensity and a succession of dry years caused marked changes in the vegetation. Annuals have usurped perennials. In extreme cases the present vegetation consists primarily of unpalatable, shallow-rooted legumes. This process has been accompanied by a greater exposure of bare soil, leading to increased soil erosion and reduced infiltration of water in the soil. Subsequent removal of grazing or the occurrence of a succession of wet years after the drought have rarely enabled the vegetation to revert to its former floristic composition and biomass (Walker et al. 1981, Breman and De Wit 1983, Sincair and Fryxell 1985, Le Houérou 1989).

Sahelian Rangeland Dynamics

Our analysis does not consider the woody layer of the vegetation, although we acknowledge its potential to interact with the herb layer. The herb layer is quite heterogeneous internally as well as being economically important as forage, and so we focus on it alone for simplicity. Its unique dynamics are illustrated below.

Box 1. Division of the herb layer of the Sahelian rangelands into 3 groups. Data from Breman et al. (1980), Cissé (1986), Le Houérou (1989), De Bie (1991). See text for further explanation.

Group I: Perennial grasses.

Examples of typical plant communities:
Community of *Andropogon gayanus* Kunth.
Community of *Cymbopogon schoenanthus* (L.) Spreng.

Main properties of dominating plant species:
* C4 photosynthesis
* High biomass per plant
* High growth rate
* "flexible response" after grazing or drought
* Vulnerable seed
* Rapidly germinating
* Homogeneous germination
* Palatable

Group II: Annual grasses.

Examples of typical plant communities:
Community of *Pennisetum pedicellatum* Trin.
Community of *Schoenefeldia gracilis* Kunth.

Main properties of dominating plant species:
* C4/C3 photosynthesis
* Moderate biomass per plant
* High growth rate
* Long growing cycle
* Vulnerable seed
* Rapidly germinating
* Homogeneous germination
* Very palatable

Group III: Annual herbs.

Examples of typical plant communities:
Community of *Borreria chaetocephala* (DC.) Hepper
Community of *Borreria stachydea* (DC.) Hutch. & Dalz.

Main properties of dominating plant species:
* C3/C4 photosynthesis
* Low biomass per plant
* Low growth rate
* Short growing cycle
* Hard, tough seeds
* Slowly germinating
* Heterogeneous germination
* Unpalatable

The herb layer of the Sahelian rangelands can be divided into 3 main groups: perennial grasses, annual grasses and annual herbs (Breman et al 1980, Cissé 1986). Box 1 gives the main characteristics of each group.

The state-and-transition formulation (Westoby et al 1989) can be used to summarize the dynamics of Sahelian rangeland vegetation. Each recognized group (perennial grasses, annual grasses, or annual herbs) consists of typical plant communities. The term "community" is defined here as a group of plants which typically co-occur in repetitive combinations of associated plants (Mueller-Dombois and Ellenberg 1974), dominated by 1 or 2 characteristic plant species which produce the highest annual biomass (Breman et al. 1980) (for example: community of *Schoenefeldia gracilis*).

Each main group of plant communities can be conceptualized as a vegetation state–an abstraction encompassing a certain amount of variation in time. Two states are separated in time by a transition–a process of vegetation change between 2 states. Transitions can be observed over a relatively small period of time (up to several years) while a state is able to persist for decades (Westoby et al 1989).

In Fig. 2 and Box 2 the Sahelian vegetation dynamics are expressed in terms of states and transitions. Figure 2 is similar to a scheme presented by Breman et al. (1980) and Cissé (1986) but we have extended it with transition T2b and process 4a and have excluded migration of species. The agro-ecological conditions under which transitions take place and the state-and-transition formulation of these transitions are hypothetical and will be further discussed in the next sections.

Application of the Cusp Catastrophe

The state and control variables of the Sahelian rangeland dynamics can now be identified. Effective rainfall and grazing intensity are useful control variables because these are the main forces driving the transitions between the 3 main vegetation states. The state variable is the vegetation community. It can be expressed by the mean annual biomass production because the production of each type of plant community (vegetation state) can be categorized in a specific yearly biomass production class, as can be deduced from data from Breman et al. (1980) and Breman and De Wit (1983). Note that the term "state variable" has been adopted from catastrophe theory, while the term "vegetation state" has been taken from the state-and-transition formulation. Figure 3 illustrates the proposed configuration of state and control variables along the axes of the cusp catastrophe model.

The figure presents an example of how to study grazing system behaviour under changing agro-ecological conditions using a vector along the cusp manifold as proposed by Loehle (1985). The transitions between Sahelian vegetation states (Fig. 2 and Box 2) are indicated by such vectors. This exercise, however, requires an exploration of assumptions and hypotheses.

Because the cusp manifold is an equilibrium manifold, the main assumption is that the 3 vegetation states (Fig. 2 and Box 2) are system equilibria. This assumption is a reasonable reflection of reality. The vegetation state of communities of perennial grasses (state I) can persist if grazing intensities are low and independent of effective rainfall. Le Houérou (1989) concluded that there is little doubt that the "primeval vegetation" of the Sahel is a

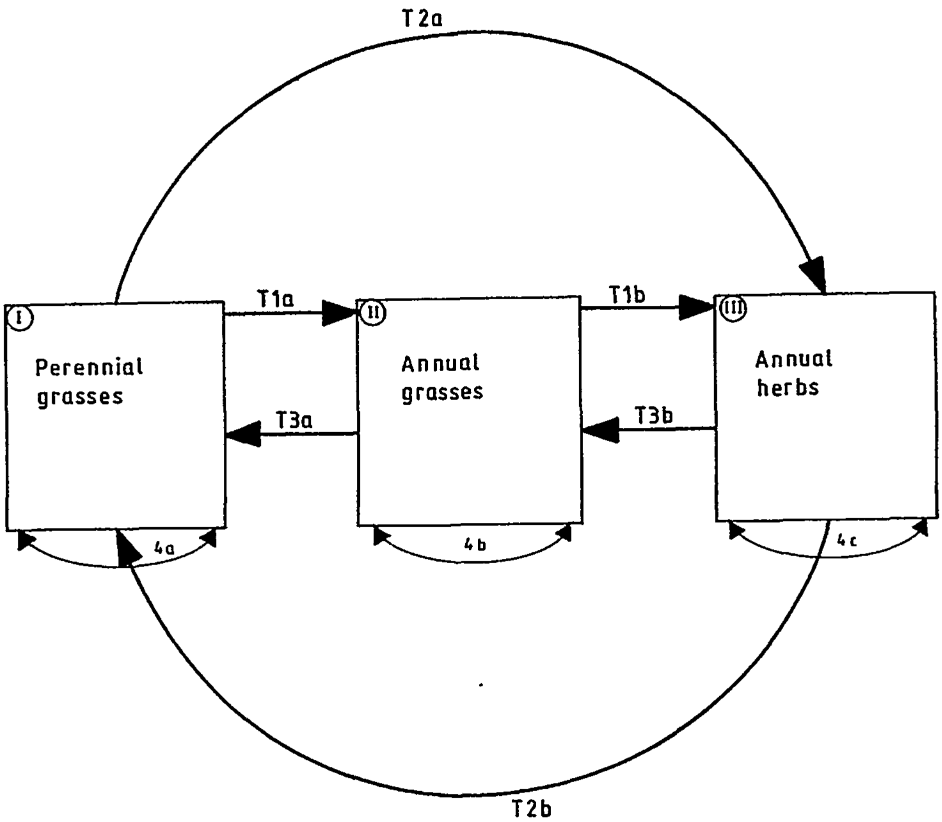

Fig. 2. A state-and-transition diagram for the herbaceous vegetation dynamics of Sahelian rangelands based on Breman et al. (1980) and Cissé (1986). The state-and-transition formulation has been taken from Westoby et al. (1989). Catalogues in Box 2.

Box 2. Catalogues for the predominantly hypothetical state-and-transitions diagram (Fig. 2). Data from Breman and Cissé (1977), Breman et al. (1980), Sinclair and Fryxell (1985) and Cissé (1986). State-and-transition formulation from Westoby et al. (1989). See text for further explanation.

Catalogue of states

State I. Communities of perennial grasses. For relevant properties of dominant plant species and examples, see Box 1, group I.

State II. Communities of annual grasses. For relevant properties of dominant plant species and examples, see Box 1, group II.

State III. Communities of annual herbs. For relevant properties of dominant plant species and examples, see Box 1, group III.

Catalogue of transitions

Transitions T1a and T1b. Gradual replacements under the influence of high or increasing grazing intensity coinciding with a period of several years with high or increasing effective rainfall. Vegetation "degradation".

Transitions T2a and T2b. Abrupt replacements. *T2a*: Vegetation "degradation" under the influence of high or increasing grazing intensity, coinciding with a period of several years of low or decreasing effective rainfall. *T2b*: Vegetation "regeneration" under the influence of low or decreasing grazing intensity, coinciding with a period of several years of low or decreasing effective rainfall.

Transitions T3a and T3b. Gradual replacements under the influence of low or decreasing grazing intensity and a period of several years of high or increasing effective rainfall. Vegetation "regeneration".

Process 4a,4b and 4c. Replacements of plant communities within states under the influence of changing grazing intensity and variable effective rainfall. These processes are not transitions according to the state-and-transition formulation, because the vegetation remains in the same state.

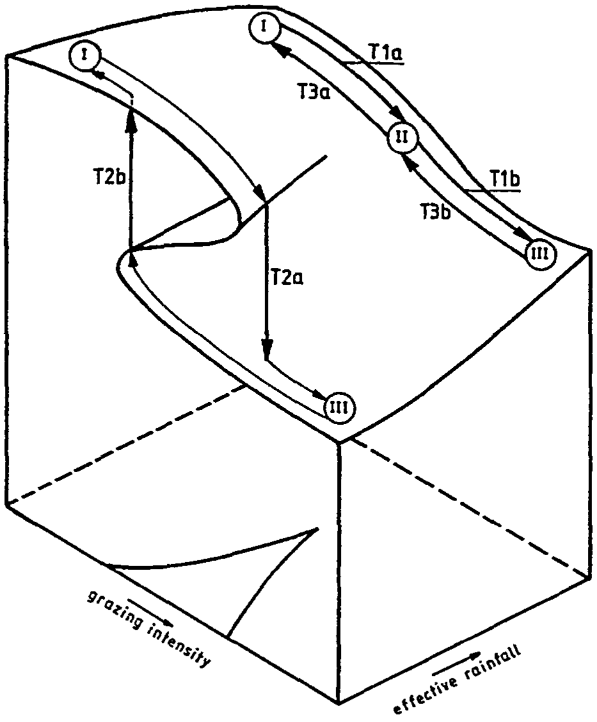

Fig. 3. The cusp catastrophe model applied to Sahelian rangeland dynamics. The vectors along the cusp manifold are the transitions as indicated in Fig. 2 and Box 2.

perennial grass steppe. It has been proved that communities of perennial grasses used to be much more abundant at times of low grazing intensity than they are at present (Boudet and Leclerq 1970, Breman and Cissé 1977, Breman et al. 1980). Further, data presented by Sinclair and Fryxell (1985) suggest that communities of perennial grasses and their accompanying high yearly biomass production can resist droughts if grazing intensities are low (or grazing management is appropriate). This implies an equilibrium. Particular vegetation states of communities of annual grasses or annual herbs (state II or state III) can persist over decades under moderate or high grazing intensities (Breman and Cissé 1977, Wickens and White 1979, Walker et al. 1981, Breman and De Wit 1983, Sincair and Fryxell 1985, Le Houérou 1989). Because these communities can survive over a much longer period than their turnover time, this also implies system equilibria (Connell and Sousa 1983). Our main hypotheses are based upon the agro-ecological conditions under which the vegetation remains in a state of equilibrium and under which continuous or discontinuous changes will take place.

If the vegetation is in state I and the grazing intensity is low for a long period of time, yearly changes in effective rainfall will not lead to transitions, but will merely result in plant communities within the same state being replaced (process 4a, Fig. 2 and Box 2). This hypothesis is strengthened by the findings of Sinclair and Fryxell (1985), who argued that in the Sahel drought alone could not have caused the dramatic vegetation transitions in the early seventies. Likewise, when the vegetation is in state III and the grazing intensity remains high, yearly changes in effective rainfall will not lead to transitions, but only to plant communities within the same state being replaced (process 4c, Fig. 2 and Box 2). This hypothesis is strengthened by the conclusions of Le Houérou (1989) and Breman and Kessler (1995) that overgrazing in the Sahel prevents the regeneration process after droughts.

During a period of high effective rainfall and if the vegetation is in state I, an increasing grazing intensity alone will lead to gradual transitions from state I to state II (T1a) and eventually from state II to state III (T1b). From state III, a decreasing grazing intensity will lead to the reversed version of the gradual transition path (T3b and T3a), provided that the effective rainfall remains high. These processes have been described for the Sahel by Breman and Cissé (1977), Breman et al. (1980) and Le Houérou (1989).

If the vegetation is in state I, a combination of several years of low effective rainfall and increasing grazing intensity will lead to catastrophic transitions from state I to state III that bypass state II (T2a). This kind of relatively rapid disappearance of communities of perennial grasses and their subsequent replacement by communities of annual herbs has been reported by several authors (Breman et al. 1980, Sinclair and Fryxell 1985). Finally, if the vegetation is in state III, a combination of the occurrence of a period of several years with low effective rainfall and a decreasing grazing intensity will lead to transitions from state III to state I that skip state II (T2b). This hypothesis will be clarified in the next section.

Catastrophe Flags

A catastrophe flag is a symptom in the behaviour of a system indicating the presence of a catastrophe (Gilmore 1981). It is therefore interesting to detect these specific catastrophic properties of the behaviour of the Sahelian rangeland ecosystem. It should be emphasized that the 5 catastrophe flags occur if the values of the control variables are within the bifurcation set. The definitions of the catastrophe flags used in this section are based on Gilmore (1981) and Lockwood and Lockwood (1993).

1) **Bimodality.** Bimodality means that an ecosystem has 2 distinct vegetation states as system equilibria. For the Sahel, these are the vegetation states of communities of perennial grasses or communities of annual herbs. Under the conditions specified by the bifurcation set, there is the risk of soil degradation such as crust formation or erosion by wind or water. If these processes occur, communities of annual herbs can persist because of their risk-spreading seed banks, heterogeneous germination and unpalatability to livestock. Under these circumstances, inferior competitors from other community types (annual grasses and perennial grasses) have difficulty in colonizing and becoming established (Breman et al. 1982, Breman and Stroosnijder 1982, Westoby et al. 1989, Laycock 1991).

Under the conditions specified by the bifurcation set, communities of perennial grasses can also persist if soil degradation processes do not occur. Once established, this type of community stabilizes the soil (Kelly and Walker 1976) by forming a network of living roots and (underground) stems, through which the plant can reproduce vegetatively. The perennial grasses may resprout after moderate grazing or a dry period; this is called a "flexible response" (De Bie 1991). The rapid sprouting or germination of perennial grasses as well as their rapid growth at the onset of the wet season, combined with a high biomass per plant give them an advantage over annual grasses and annual herbs. Additional factors which may help them to outcompete the annual grasses are the relatively large amount of dead foliage and stalks among the green leaves which protects them against grazing (Westoby 1979/80, Prins 1988), and their usually inferior forage quality (Breman et al. 1980, Stafford Smith and Morton 1990).

Communities of annual grasses cannot persist under the conditions specified by the bifurcation set. Annual grasses are inferior competitors because these plants are preferred by livestock (Breman et al. 1980, Le Houerou 1989). Furthermore, there is evidence that their seeds do not remain viable in the soil for more than 1 year (Breman et al. 1980, Cissé 1986), which means that the seeds produced in the rainy season, their survival rate in the soil during the dry season, and their germination rate in the following rainy season, determine the probability of plants flowering in that season. A period of several years with low effective rainfall, combined with a moderate grazing intensity, prevents establishment after germination and leads to rapid depletion of the seed bank of these annual communities. The critical importance of seed bank dynamics for the stability characteristics of a grazing system has already been clearly recognized by Breman et al. (1980) and Cissé (1986) for the Sahel and by Hodgkinson (1991) for Southeast Australia.

2) **Inaccessibility.** The middle sheet of the cusp catastrophe manifold is mathematically characterized as an unstable equilibrium (see **Appendix**, Fig. 4). Therefore, this part of the equilibrium surface is referred to as inaccessible. This is illustrated by the arrows diverging from the middle sheet (Fig. 1).

The communities of annual grasses–with the accompanying yearly biomass production class of, for instance, an average of 1.5 to 3.0 t $ha^{-1}.yr^{-1}$ under a rainfall regime of 550 mm yr^{-1} (Breman et al. 1980) cannot persist under the conditions specified by the bifurcation set, as explained in the former section. Assuming a constant grazing intensity and effective rainfall regime, and depending on possibly very small differences between initial values of the state variable, the system will either shift to the upper surface (vegetation state of communities of perennial grasses with a higher yearly biomass production) or to the lower surface (vegetation state of communities of annual herbs with a lower yearly biomass production).

3) **Sudden jumps.** Sudden jumps are seen when a trajectory reaches an edge of the cusp and jumps to the alternative sheet or state. Note that the jump is a jump of equilibria and not necessarily of the state variable. This means that spurts in temporal data can be expected. However, this may be difficult to detect because the detection of changes is scale-dependent (Friedel 1994) or because the state variable may lag. Although the catastrophic jump is depicted in the cusp surface as occuring instantaneously, an actual change in a state variable will always take a certain amount of time. This amount of time might be dependent on properties not inherent in the model.

The rapid disappearance of communities of perennial grasses and their subsequent replacement by communities of annual herbs as reported by Breman et al. (1980) and Sinclair and Fryxell (1985) can be interpreted as a sudden jump of the state variable from the upper sheet to the lower sheet of the cusp catastrophe figure. This process is comparable to transition T2a (Fig. 2 and 3). Transition T2b is the hypothetical reversed transition (Figs. 2 and 3). If the vegetation is in the annual herb state and effective rainfall is low, a decreasing grazing intensity will lead to a transition from that state to the perennial grass state that skips the annual grass state. This means that perennial grasses may sprout again or recolonize the area through seeds imported by wind, water, or animals because the area is relieved from grazing impacts that result in high plant mortality and soil compaction. Under these conditions the perennial grasses eventually establish and stabilize the soil, and annual communities will no longer persist. This process may take decades if the soil first has to recover from crust formation or erosion (Le Houérou 1989, Laycock 1991). The lack of evidence of rapid transitions from the annual herb state to the perennial grass state in the Sahelian region is probably due to this decades-long recovery process, in relation to the time-scale of observation.

4) **Divergence.** This flag arises when relatively small changes (or close starting points) in the control variables result in widely separated final states.

It is not too difficult to conceive of small differences in rainfall or grazing at a certain point in time subsequently leading to the development of a rangeland vegetation consisting of communities of perennial grasses or annual herbs. For example, the performance of the rainy season is critical for the establishment of vegetation (Breman et al. 1980, Prins 1988, Prins and Loth 1988). A rainy season starting with frequent, small showers favours a community of rapidly germinating, fast growing annual and perennial grasses. One that starts with only 1 or 2 large showers results in the germination of both fast and slow growing plants, leading to a community of perennial grasses, annual grasses, and annual herbs. A third possibility is a rainy season that starts with small showers, interrupted by long, dry intervals, resulting in communities of predominantly annual herbs at the end of that rainy season. This, plus small differences in grazing intensities which also influence the establishment of vegetation in the beginning of the rainy season, has consequences for the long term development of the community.

5) **Hysteresis.** Jumps at distinct values of the control variables, when the latter follow either an increasing or a decreasing path, is referred to as hysteresis. There are 2 ways to formulate this property in relation to the rangeland ecosystem (Lockwood and Lockwood 1993). The first is the formulation that transitions between states are virtually irreversible without substantial human intervention (Friedel 1991). As mentioned earlier, the transition from a vegetation community of annual herbs to another state is not necessarily possible within a reasonable period of time (several years) if the soil has to recover from soil degradation such as crust formation or erosion. Soil and water conservation measures may then be necessary, as is widely recognized for the Sahelian region (Le Houérou 1989, Stroosnijder 1992, Hien 1995).

Another way to formulate hysteresis is to envisage "decline" and "recovery" as following different paths or trajectories (Friedel 1991, Laycock 1991), as was earlier recognized in semi-arid pastoral ecosystems [e.g. by Breman et al. (1980), Sinclair and Fryxell (1985), Ellis and Swift (1988) and Behnke and Scoones (1992)]. This can be illustrated with the following example from the Sahel. The perennial grass *Andropogon gayanus* almost disappeared from a specific site after a disturbance of 2 dry years (1972-1973) and was subsequently replaced by annual herbs like *Borreria* spp. From 1976 onwards the rapidly germinating annual grasses *Schoenefeldia gracilis* and *Diheteropogon hagerupii* became increasingly important at that site. From 1979 young plants of *Andropogon gayanus* could again be observed regularly, but in terms of biomass they were not yet important (Breman and Cissé 1977, Breman et al. 1980). Data about grazing intensity related to the system dynamics presented in this specific example is missing in the literature. Given the system dynamics of the example and the model we have presented, the hypothesis would be that the dry period coincided with increasing grazing intensity and that the subsequent period of higher rainfall coincided with decreasing grazing intensity.

Discussion

Catastrophe theory offers an interesting framework on which ecosystem description and analysis can be based. The application of cusp catastrophe theory to the Sahelian rangeland vegetation dynamics generates a conceptual model which describes both the continuous and the discontinuous processes occurring in this ecosystem. Additionally, this application appears to be a useful tool for translating rather vague concepts into a verifiable format by generating hypotheses about the agro-ecological conditions under which the Sahelian vegetation remains in a state of equilibrium and under which continuous or discontinuous changes, including threshold values, will take place.

A key hypothesis in this paper is that communities of annual grasses do not persist under the conditions specified by the bifurcation set because their seed bank is ultimately eliminated.

The 5 so-called catastrophe flags will only occur when the values of the control variables are *within* the bifurcation set. There are, however, 3 additional flags which can be manifest when the control variables are *outside* the bifurcation set: divergence of linear response, critical slowing down, and anomalous variance (Gilmore 1981). The divergence of linear response flag implies that perturbations of the control variables near an edge of the cusp will lead to large oscillations of the state variable. There is little doubt that large variations in the state variable of rangelands occur. Breman et al. (1980) observed a large year-to-year variation in total biomass and in relative importance of dominant species at the end of the rainy season. Kelly and Walker (1976) and Friedel (1991) observed that yearly biomass and forage composition fluctuates more in areas with a high grazing impact than in areas with a low grazing impact. The management implications of increased variation in the state variable are obvious. This flag would mean that the manager can not reliably predict the extent to which grazing must be reduced or increased in order to generate a catastrophic transition. Thus, the use of particular case studies from sites within the Sahel as a basis for anticipating the dynamics in another area within the region is hazardous. The grazing intensity that resulted in a catastrophic transition from perennial grasses to annual herbs at 1 site could differ markedly from that seen at another, seemingly identical, site.

Critical slowing down means a delayed recovery of equilibrium in the case of perturbation of the control variables when these approach the bifurcation set. This flag does not concern the magnitude of change (like the last flag) but the rate of re-equilibrium of the state variable. Wissel (1984) proved theoretically that the characteristic return time to an equilibrium of natural communities in ecosystems increases when the control variables approach a bifurcation point. Anomalous variance means that the variance of a state variable may increase near a catastrophe. The criteria anomalous variance and oscillations due to the divergence of linear response have the same expected pattern when the control variables approach (and move through) the bifurcation set. Large oscillations due to the divergence of linear response will presumably be manifest as anomalous variance. As the interpretation of this flag remains primarily a statistical curiosity without obvious additional management implications, this catastrophe flag will not be discussed further. It is not known whether the additional catastrophe flags mentioned above have any predictive value for rangeland vegetation dynamics.

The cusp catastrophe model does not show the spatial changes in vegetation patterns of the rangeland ecosystem following a north-south transect from the Sahara desert into the Sudanian savannas or vice versa. It is tempting to fit data to the model on a spatial basis, because of the gradient of the average amount of rainfall per year. But it is the development of the ecosystem in time within the Sahel zone which defines the basic properties of the system, and not the spatial changes in vegetation patterns. Therefore, the conceptual model presented here is location-specific. What could be stated, however, is that the chance of gradual transitions between vegetation states increases with increasing annual rainfall, thus following a north-south transect.

The exact boundaries between the vegetation states on the cusp manifold (Fig. 3) can only be indicated after long-term empirical data have been collected and fitted statistically to the conceptual model. However, such an indication is not necessary for understanding the application of the cusp catastrophe theory to the dynamics of the Sahelian rangeland ecosystem and its management implications.

Future research could be based on statistical fitting of data to this conceptual catastrophe model. Lockwood and Lockwood (1991) developed such a method and accurately predicted (referring to the ability of a model output to match observed dynamics) changes in grasshopper population dynamics using the cusp catastrophe model and thereby showed that catastrophe theory is capable of generating quantitatively testable hypotheses. However, the result of this exercise did not provide any biological or ecological insights because catastrophe theory fails to explain the underlying causes of catastrophic behaviour. As Saunders (1980) points out, the advantage of catastrophe theory lies in the modelling of systems with intractable complex inner workings. In this case, however, we are more concerned about a mechanistic explanation of catastrophic dynamics because we think that this would partly answer the urgent management question on the conditions under which catastrophic vegetation changes can be expected. Rietkerk and Van de Koppel (submitted) created a mathematical model showing that some important properties of catastrophic behaviour can already be explained by common plant-soil relations.

Another approach in future research would be to test the qualitative hypotheses generated by the conceptual model. A series of controlled and systematic studies to determine if the transitions described in this paper are empirically demonstrable would be very useful. Finally, the detection of additional catastrophe flags, such as divergence of linear response and critical slowing down, could provide a possible means of devising an early warning of approaching thresholds.

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Appendix

This is a description of the geometry of the cusp catastrophe manifold. The collection of potential functions V(x) determining the cusp catastrophe is given by the equation:

$$V(x)= 0.25\,x^4 + 0.50\,px^2 + qx \qquad (1)$$

x is the state variable and p and q are the control variables. The familiar cusp catastrophe manifold is the configuration of the minima and maxima of the potential functions and is determined by:

$$V'(x)= x^3 + px + q = 0 \qquad (2)$$

The bifurcation set is the subset of equation 2 for which the following equation is also satisfied:

$$V''(x)= 3x^2 + p= 0 \qquad (3)$$

In Fig. 4 the potential functions V(x) are presented for 3 different pairs of values of the control variables p and q which are indicated as points with corresponding numbers in an illustration of the parameter surface with the bifurcation set.

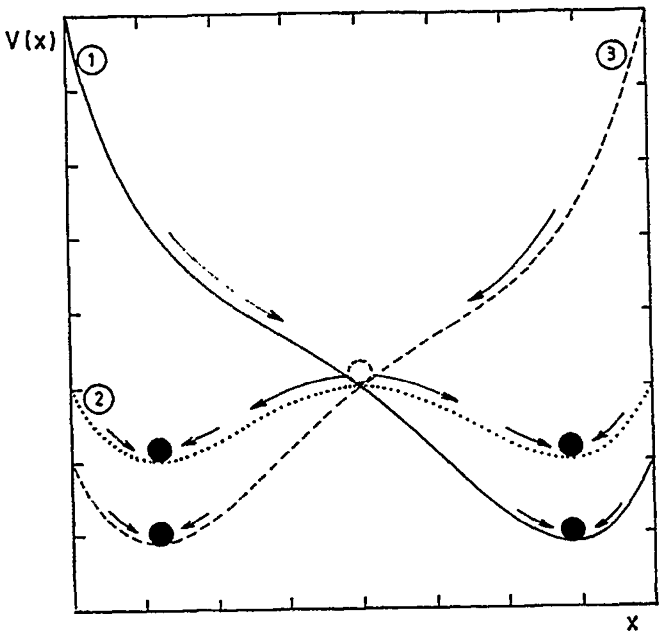

Fig. 4a

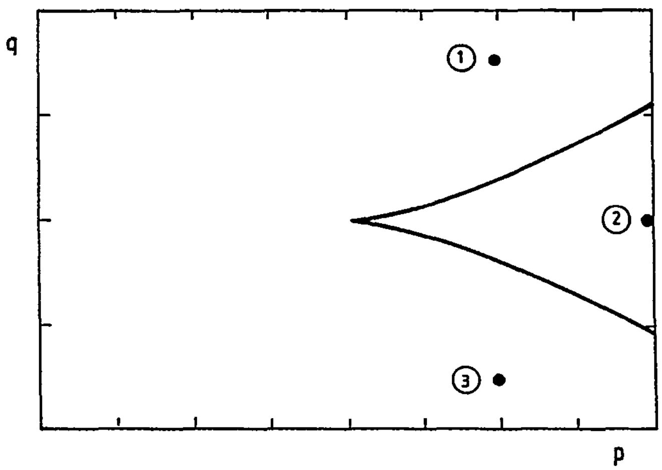

Fig. 4b

Fig. 4. (a) The curves of the potential function V(x) for 3 different pairs of values of the control parameters p and q. The 3 different pairs of values of the control variables are indicated by the numbers 1, 2 and 3. The light circle with the diverging arrows represents the location of an unstable system equilibrium. The dark circles, with converging arrows represent local minima of the potential function and therefore stable system equilibria. (b) The pairs of values of the control parameters p and q are indicated on the parameter surface with the bifurcation set by points with the corresponding numbers 1, 2 and 3.