Site-specific properties and irreversible vegetation changes in semi-arid grazing systems

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There is an urgent need to develop a mechanistic understanding of how site-specific properties can lead to irreversible vegetation changes. We show, by means of a bifurcation analysis of two mathematical models, how site-specific properties determine the resilience of vegetation changes in semi-arid grazing systems. The models predict that if available soil water limits plant growth, the vegetation supported by sandy soils is generally resilient to herbivore impact and rainfall fluctuations, unlike the vegetation on clayey soils. This depends on the capacity of vegetation communities to improve the structural and water-holding capacities of the soil. In contrast, if plant growth is nutrient limited, vegetation on sandy soils is generally not resilient to herbivore impact and fluctuations in external nutrient input, unlike the vegetation supported by clayey soils. This is affected by the nutrient retention capacity of vegetation communities. We stress the applicability of the general theory provided by this model to the Sahel environment. The model predictions are consistent with field observations documented in the literature.

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Concepts and models of vegetation change in semi-arid grazing systems have come about as a result of more than a decade of thinking about resilience (e.g. Walker et al. 1981, Walker and Noy-Meir 1982). In its original, qualitative sense, resilience refers to the property of a system that the population density tends to remain within a certain domain with only one attracting equilibrium in the face of environmental fluctuations (Holling 1973, Yodzis 1989). Applied to semi-arid grazing systems this means that a system is resilient if vegetation changes driven by herbivory or environmental fluctuations are continuous and reversible. It should thereby make no difference whether these environmental fluctuations are large and frequent or not.

Closely related to this definition of resilience is the recent notion that African grazing systems are intrinsically resilient, because they have persisted for decades or more despite large and frequent environmental fluctuations (Ellis and Swift 1988, Abel and Blaikie 1989, Behnke and Scoones 1992). This is usually meant in the sense that there is some sort of in-built resistance to land degradation in these systems and that vegetation change is mainly determined by rainfall variations and not by herbivory. This implies that when vegetation is drastically reduced as a result of episodic intense herbivory during drought, it will nevertheless always recover if periods with higher rainfall follow. It is on these assumptions that recent, major shifts in pastoral development strategies are being based (Scoones 1994).

Ironically, it is an undeniable reality that these systems exhibit some of the worst examples of apparent degradation. Vegetation changes in semi-arid grazing systems have been found to be discontinuous and practically irreversible (Sinclair and Fryxell 1985, Westoby et al. 1989, Friedel 1991, Laycock 1991, Stafford Smith and Pickup 1993, Rietkerk et al. 1996). This suggests that more than one attracting equilibrium exists and that the vegetation is not resilient to herbivore impact and environmental fluctuations.

Apparently, perceptions of vegetation changes are temporally and spatially scale-dependent (Friedel 1994), or some semi-arid grazing systems are resilient and others are not (Walker et al. 1981). Consequently, the danger is manifest that concepts of vegetation change derived from resilient systems are being applied wrongly to non-resilient systems and vice versa. It is within this context that there is an urgent need to develop a thorough understanding of the differences between these systems based on a general, mechanistic theory (Illius and Hodgson 1996, Stafford Smith 1996).

Plant-soil interactions commonly operating in semi-arid grazing systems may cause positive feedback loops between reduced plant density and reduced resource availability. As a result, herbivory or environmental fluctuations may trigger vegetation changes that are discontinuous and irreversible. This insight was derived from a general, graphical analysis of two models (Rietkerk and Van de Koppel 1997), considering the shape of the feedback relation between water infiltration or nutrient retention and plant density. The general assumption on which these models are based is that either water or nutrients limit plant growth (Breman and De Wit 1983). In this paper we will investigate which site-specific properties may lead to these discontinuous and irreversible vegetation changes, with the aim to elucidate the concept of resilience as applied to semi-arid grazing systems. This is done by means of a bifurcation analysis of the two models mentioned earlier. Therefore, we specify the explicit mathematical formulation of the two models, and briefly review the graphical analysis.

Water-limitation model

Let P and W denote plant density and soil water availability, respectively. The rate of change of both plant density and soil water availability is represented by the differential equations:

$$\frac{dP}{dt} = g(W)P - (d+b)P \tag{1}$$

$$\frac{dW}{dt} = W_{in}(P) - c(W)P - r_W W \tag{2}$$

where $g(W)$ is specific plant growth as a function of soil water availability, d is specific plant loss due to mortality and b is specific plant loss due to herbivory. Plant loss due to mortality is assumed to be density independent. We assume a linear functional response of the herbivore to changes in forage availability. Plant loss due to herbivory is kept constant; herbivore density is independent of plant density. In other words, all (re)production and mortality is balanced by removals or additions. This is a good approximation to management practices in grazing systems (Noy-Meir 1975). $W_{in}(P)$ describes water infiltration into the soil as a function of plant density and $c(W)$ the specific soil water uptake by the plants as a function of soil water availability. The specific soil water loss due to soil evaporation and deep percolation (r_W) is considered constant.

We assume that specific plant growth and specific soil water uptake are both saturation functions of soil water availability. A specific example of a saturation function is the Michaelis equation. An additional assumption is that specific plant growth increases linearly with increasing specific soil water uptake (De Wit 1958) and is at its maximum at full plant turgor, when the availability of soil water permits maximum specific soil water uptake. We can thus write

$$g(W) = g_{max} \frac{W}{W + k_1} \tag{3}$$

and

$$c(W) = c_{max} \frac{W}{W + k_1} \tag{4}$$

where g_{max} is the maximum specific plant growth, c_{max} the maximum specific soil water uptake by the plants and k_1 is a half saturation constant. The relationship between water infiltration into the soil and plant density is given by

$$W_{in}(P) = PPT \frac{P + k_2 W_0}{P + k_2} \tag{5}$$

(Walker et al. 1981). Here PPT stands for rainfall, W_0 is the minimum water infiltration in the absence of plants, expressed as a proportion of the rainfall, and k_2 is a half saturation constant (Fig. 1A). Empirical evidence for the shape of this feedback relation can be found in Van Wijngaarden (1985).

Nutrient-limitation model

The nutrient-limitation model has a similar structure as the water-limitation model. Here, N stands for soil

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nutrient availability. A constant fraction of plant losses due to mortality (not induced by herbivory) is assumed to be shunted directly into the nutrient pool and is subsequently available for plant growth (cf. DeAngelis 1992). The rate of change of both plant density and soil nutrient availability is represented by the differential equations:

$$\frac{dP}{dt} = g(N)P - (d+b)P \qquad (6)$$

$$\frac{dN}{dt} = N_{in} - c(N)P - r_N(P)N \qquad (7)$$

where $g(N)$ is specific plant growth as a function of soil nutrient availability and N_{in} is the nutrient release from the geochemical cycle which is considered independent of plant density. $c(N)$ stands for the net plant specific soil nutrient loss as a function of soil nutrient availability. $r_N(P)$ is the specific soil nutrient loss due to water and wind erosion, which is a function of plant density. The parameters d and b follow the water-limitation model.

We now assume that specific plant growth is a Michaelis function of soil nutrient availability:

Plant density P

Fig. 1. (A) The shape of the feedback relation between water infiltration W_{in} and plant density P. Parameter values: $PPT = 2$, $k_2 = 5$, $W_0 = 0.2$. (B) The shape of the feedback relation between the specific nutrient loss r_N and plant density P. Parameter values: $r_{N,max} = 0.5$, $k_2 = 25$. Symbols as in Table 1.

$$g(N) = g_{max}\frac{N}{N+k_1} \qquad (8)$$

The parameters g_{max} and k_1 follow the water-limitation model. $c(N)$ consists of two terms: the specific soil nutrient uptake by the plants as a Michaelis function of soil nutrient availability and the specific nutrient release from plant mortality. Specific plant growth increases linearly with increasing specific soil nutrient uptake and is at its maximum if the availability of soil nutrients permits maximum specific soil nutrient uptake. We can thus write

$$c(N) = c_{max}\frac{N}{N+k_1} - d\frac{c_{max}}{g_{max}} \qquad (9)$$

The parameter c_{max} follows the water-limitation model. Note that the factor $d \cdot c_{max}/g_{max}$ is the nutrient release as a consequence of plant mortality d, whereby g_{max}/c_{max} is the C/N ratio of the plant material. The relationship between the specific soil nutrient loss due to water and wind erosion and plant density is given by
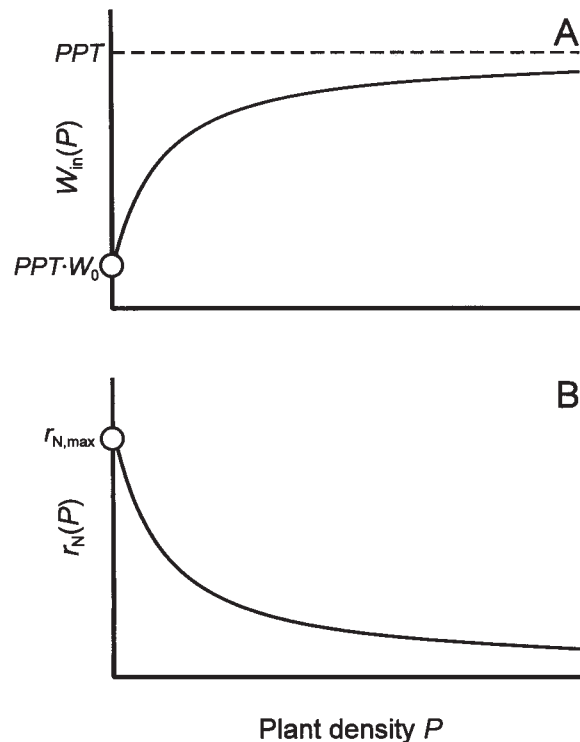
$$r_N(P) = r_{N,max}\frac{k_2}{k_2+P} \qquad (10)$$

Here $r_{N,max}$ stands for the maximum specific nutrient loss when plant density is zero, and k_2 is a half saturation constant (Fig. 1B). Empirical evidence for the shape of this feedback relation can be found in Elwell and Stocking (1974, 1976). Table 1 provides an overview of the symbols used, with their interpretation and possible units.

Zero-isoclines and functional states

We briefly review the graphical analysis of these models using zero-isocline representations in the phase planes (Fig. 2) (Rietkerk and Van de Koppel 1997). Analytically, the zero-isoclines can be obtained by setting $dP/dt = 0$, $dW/dt = 0$ and $dN/dt = 0$ (see Appendix for analytical details). The graphical combination of the two resource isoclines and the two plant isoclines respectively, results in one curved resource isocline and one straight, vertical plant isocline for both models in each phase plane. The system may be either continuously or discontinuously stable under grazing (cf. Noy-Meir 1975), depending on the shape of the resource isocline. In continuously stable systems the resource isocline has a negative slope, as a consequence of enhanced resource uptake with increasing plant density (Fig. 2A and 2B). In discontinuously stable systems the resource isocline has a positive slope, but only at low plant density (Fig. 2C, 2D and 2E). This is because only

Table 1. A survey of the symbols used, with their interpretation and possible units.

Symbol	Interpretation	Unit
P	Plant density	$g\ m^{-2}$
W	Soil water	mm
N	Soil nutrients	$g\ m^{-2}$
g_{max}	Maximum specific plant growth	$(g\ g^{-1})\ d^{-1}$
k_1	Half saturation constant of specific plant growth and water or nutrient uptake	mm or $g\ m^{-2}$
d	Specific loss of plant density due to mortality	d^{-1}
b	Specific loss of plant density due to grazing	d^{-1}
W_{in}	Water infiltration into the soil	$mm\ d^{-1}$
PPT	Rainfall	$mm\ d^{-1}$
k_2	Rate at which infiltration increases or specific nutrient loss decreases with plant density	$g\ m^{-2}$
W_0	Minimum water infiltration (in the absence of plants) expressed as a proportion of the rainfall	
c_{max}	Maximum specific water or nutrient uptake	$mm\ g^{-1}\ m^2\ d^{-1}$ or $g\ g^{-1}\ d^{-1}$
r_W	Specific loss of soil water through percolation and evaporation	d^{-1}
N_{in}	Nutrient input	$g\ m^{-2} d^{-1}$
r_N	Specific nutrient loss	d^{-1}
$r_{N,max}$	Maximum specific nutrient loss	d^{-1}

at low initial plant density an increase in plant density results in a relatively large increase of net resource input into the system (Fig. 1A and 1B). Five ecologically relevant functional states can be distinguished, depending on the shape of the resource isocline and the level of herbivory.

Undergrazed (type I) state (Fig. 2A)

In continuously stable systems, two equilibria exist at relatively low levels of herbivory: one stable internal equilibrium at high plant density and one unstable boundary equilibrium with no plants. If plants are present, the system always evolves to the internal equilibrium. Increasing the level of herbivory results in a continuous decrease of equilibrium plant density.

Overgrazed state (Fig. 2B)

At relatively high levels of herbivory there is only one equilibrium in continuously stable systems: the stable boundary equilibrium with no plants. Consumption of plants by herbivores exceeds biomass production, or, in other words, resource levels are insufficient for the plant to compensate for herbivore consumption. Lowering the level of herbivory leads to a continuous increase of equilibrium plant density.

Undergrazed (type II) state (Fig. 2C)

In discontinuously stable systems, a single stable equilibrium exists at relatively low levels of herbivory: the internal equilibrium at high plant density. This functional state is comparable with the undergrazed (type I) state in continuously stable systems. In discontinuously stable systems, however, increasing the level of herbivory results in discontinuous effects.

Alternate stable states (Fig. 2D)

Two stable equilibria exist at intermediate levels of herbivory in discontinuously stable systems: the boundary equilibrium with no plants and the internal equilibrium at high plant density. The two domains with different attracting equilibria occurring in the phase plane are separated by a separatrix. For initial values of plant density and amounts of resources under the separatrix, the system moves to the boundary equilibrium. For initial values above the separatrix, the system moves to the stable internal equilibrium. A disturbance (e.g. fire) may carry plant density or resource levels below or above certain breakpoint values as is indicated by the separatrix.

Stably degraded state (Fig. 2E)

Only one stable equilibrium exists at relatively high levels of herbivory in a discontinuously stable system:

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the boundary equilibrium with no plants. This state is comparable with the overgrazed state in a continuously stable system. However, while lowering the level

of herbivory in the overgrazed situation leads to a continuous increase of equilibrium plant density, lowering herbivory to an intermediate level in this situation has no effect at all. The system can only be restored if plant density or resource levels are increased beyond certain breakpoint levels or if the level of herbivory is dramatically decreased.

Note that the level of herbivory, which determines the position of the plant isocline, is human controlled. In contrast, the shape and position of the resource isocline are determined by prevailing ecological site conditions. Thus, site-specific properties play a vital role in determining whether the system is continuously or discontinuously stable.

Bifurcations

We showed that parameter variation affects the existence and stability properties of equilibria. Each time that such new qualitative behaviour is established, a so-called point of bifurcation is reached (e.g. Edelstein-Keshet 1988, Yodzis 1989). So, a point of bifurcation is a certain combination of parameter values at which the qualitative behaviour of a system will change. These points can be derived from the solutions of corresponding analytical criteria. For each of the two models, two of such criteria can be recognized.
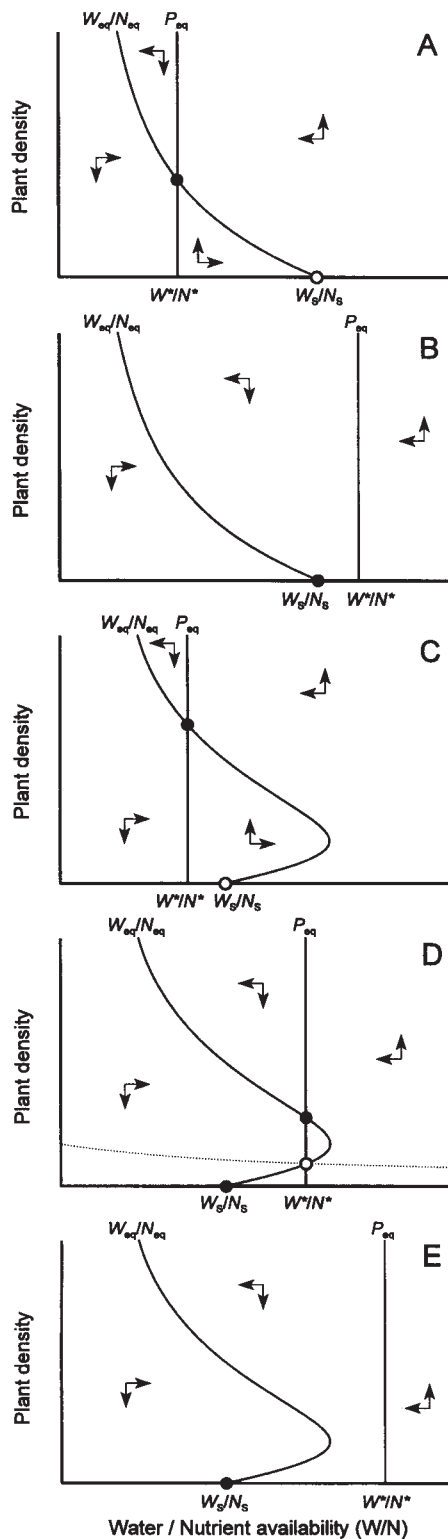
Fig. 2. Phase planes representing five functional states. Phase planes with W on the horizontal axis represent water-limited systems. Phase planes with N on the horizontal axis represent nutrient-limited systems. The combined resource isocline is indicated by W_{eq}/N_{eq} and the combined plant isocline by P_{eq}. W_s/N_s is the point where the resource isocline intersects with the $P = 0$ axis and W^*/N^* is the point where the plant isocline intersects with this axis. See Appendix for further analytical details. We change the level of herbivory b, water infiltration and specific nutrient loss (both in the absence of plants, denoted by W_0 and $r_{N,max}$, respectively), and the rate at which infiltration increases or specific nutrient loss decreases with plant density (k_2). Open circles indicate unstable system equilibria, closed circles indicate stable equilibria. Vectors indicate the direction of change given a certain starting point. The interactions between water infiltration or nutrient retention and plant density potentially give rise to the existence of alternate stable states and threshold effects. Herbivory may trigger a positive feedback between reduced plant density and reduced resource availability. (A) Undergrazed (type I) state. (B) Overgrazed state. (C) Undergrazed (type II) state. (D) Alternate stable states. (E) Stably degraded state. Parameter values: (A–E) $g_{max} = 0.5$, $k_1 = 3$, $d = 0.1$, $c_{max} = 0.05$. In case of water-limitation: $PPT = 2$, $r_W = 0.1$. In case of nutrient-limitation: $N_{in} = 1$. (A–B) In case of water-limitation: $W_0 = 0.9$, $k_2 = 25$. In case of nutrient-limitation: $r_{N,max} = 0.2$, $k_2 = 400$. (C–E) In case of water limitation: $W_0 = 0.2$, $k_2 = 5$. In case of nutrient-limitation: $r_{N,max} = 0.5$, $k_2 = 25$. (A–E) The values of b are in case of water- and nutrient-limitation respectively: (A) $b = 0.15$; $b = 0.15$, (B) $b = 0.35$; $b = 0.25$, (C) $b = 0.15$; $b = 0.05$, (D) $b = 0.25$; $b = 0.12$, (E) $b = 0.35$; $b = 0.15$. Symbols as in Table 1.

When will plants be successful in colonizing bare areas?

If plants are able to successfully colonize bare areas, the boundary equilibria are unstable (Fig. 2A and 2C). If plants do not succeed, these equilibria are stable (Fig. 2B, 2D and 2E). Plants will succeed in invading bare soil if their growth exceeds their losses. In case of the water-limitation model, specific growth equals $g_{max}(W/(W + k_1))$ (eq. 3). In bare soil, water levels equilibrate at $W = W_s = PPT(W_0/r_W)$ (eq. A3, Appendix). Consequently, plants will be able to invade whenever

$$g_{max} \frac{W_s}{W_s + k_1} > (d + b) \tag{11}$$

from which can be derived that

$$\frac{k_1(d + b)}{g_{max} - d - b} < PPT \frac{W_0}{r_W} \tag{12}$$

So, the point of bifurcation is reached if $W^* = W_s$ (eq. A1, Appendix), as illustrated in Fig. 2.

Likewise, in case of the nutrient-limitation model, growth equals $g_{max}(N/(N + k_1))$ (eq. 8). If plants are absent, then $N = N_s = N_{in}/r_{N,max}$ (eq. A4, Appendix), from which can be derived that plants will be able to invade bare areas if

$$\frac{k_1(d + b)}{g_{max} - d - b} < \frac{N_{in}}{r_{N,max}} \tag{13}$$

So, this point of bifurcation is reached if $N^* = N_s$ (eq. A2, Appendix), as illustrated in Fig. 2. This leads to the general conclusion that the stability properties of the boundary equilibrium will change if the point where the resource isocline crosses the $P = 0$ axis is equal to the point where the plant isocline crosses this axis.

When will the plant population collapse?

Consider the case of an increasing level of herbivory, leading the system from an undergrazed (type II) state (Fig. 2C), to a stably degraded state (Fig. 2E). The system will then pass through the alternate stable state situation (Fig. 2D). The plant population will suddenly collapse at the point where the plant isocline is tangential to the hump of the resource isocline. Hereby, the number of internal equilibria will change from two (alternate stable states) to zero (stably degraded state). This is further illustrated in Fig. 3. Note that sudden jumps of plant density equilibria occur at distinct levels of herbivory, when the latter follows either an increasing or decreasing path. This discontinuous property is often referred to as hysteresis (Lockwood and Lockwood 1993). The function describing the relation be-
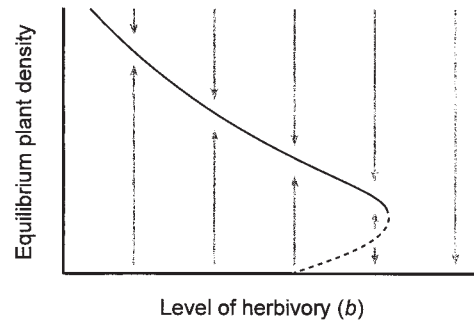

Level of herbivory (b)

Fig. 3. An example of a catastrophe fold showing the relation between equilibrium plant density P_{eq} and the level of herbivory b. Sudden jumps of plant equilibria occur at distinct levels of herbivory, when the latter follow either an increasing or decreasing path. This property is referred to as hysteresis. Parameter values: $g_{max} = 0.5$, $k_1 = 3$, $d = 0.1$, $c_{max} = 0.05$. In case of water-limitation: $PPT = 2$, $r_W = 0.1$, $W_0 = 0.2$, $k_2 = 5$. In case of nutrient-limitation: $N_{in} = 1$, $r_{N,max} = 0.5$, $k_2 = 25$. Symbols as in Table 1.
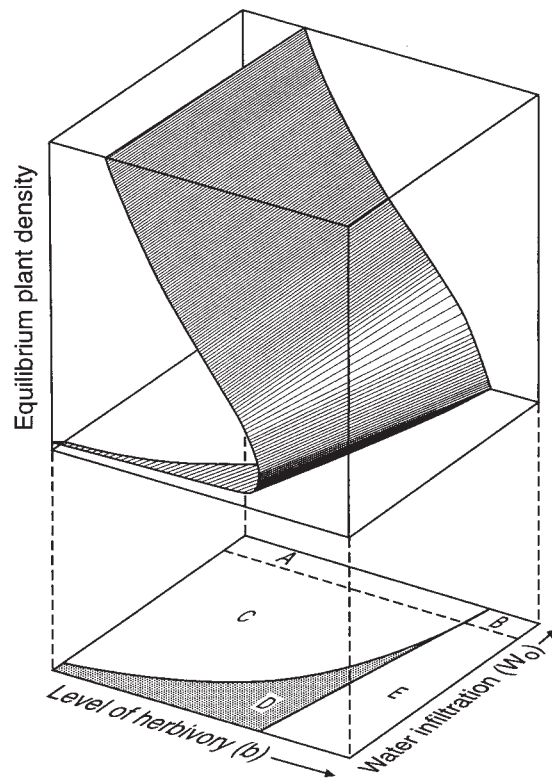

Fig. 4. An example of an equilibrium manifold showing the equilibrium plant density P_{eq} as a function of the level of herbivory b and water infiltration W_0. Parameter values: $g_{max} = 0.5$, $k_1 = 3$, $d = 0.1$, $PPT = 2$, $k_2 = 5$, $c_{max} = 0.05$, $r_W = 0.1$. Symbols as in Table 1. The bifurcation set, outlined by the shaded area in the parameter plane, indicates for which parameter values alternate stable states exist. The dashed line indicates for which parameter combinations a trajectory through the parameter plane will move through the bifurcation set while increasing or decreasing the level of herbivory. A = Undergrazed (type I) state, B = Overgrazed state, C = Undergrazed (type II) state, D = Alternate stable states, E = Stably degraded state (see Fig. 2).
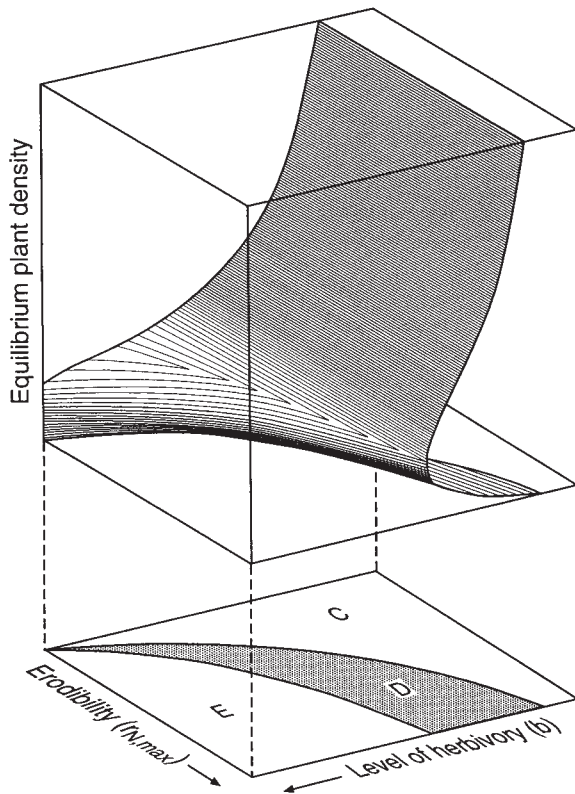
Fig. 5. An example of an equilibrium manifold showing the equilibrium plant density P_{eq} as a function of the level of herbivory b and maximum specific nutrient loss $r_{N,max}$. The maximum specific nutrient loss can be interpreted as erodibility of the soil (see text). Parameter values: $g_{max} = 0.5$, $k_1 = 3$, $d = 0.1$, $N_{in} = 5$, $c_{max} = 0.05$, $k_2 = 1$. Symbols as in Table 1. The bifurcation set is indicated in the parameter plane. C = Undergrazed (type II) state, D = Alternate stable states, E = Stably degraded state (see Fig. 2).

two lines on the parameter planes are horizontal projections of the "folded-over" parts of the equilibrium manifold. Note that each point on the parameter surface indicates a certain combination of parameter values. The position of each point in relation to those of the two lines specifies the functional state of the system. The shaded areas (so-called bifurcation sets), contain those parameter values for which alternate stable states exist.

For parameter values above the dashed line in Fig. 4, a trajectory through the parameter plane while increasing or decreasing the level of herbivory will not move through this bifurcation set. In that case the system is continuously stable. Thus in Fig. 5, all the trajectories through the parameter plane while increasing or decreasing the level of herbivory will move through the bifurcation set. In that case the system is discontinuously stable.

Results

The bifurcation sets are also mathematically defined (criteria 12 and 13 and the numerically solved criteria). Using these criteria we can investigate the effects of parameter changes on the shape and position of the bifurcation sets, without deriving the shapes of the equilibrium manifolds first (Figs 6 and 7, for the water-limitation and nutrient-limitation model, respectively). The horizontal dashed lines indicate parameter combinations for which a trajectory through the parameter plane will move through the bifurcation set while increasing or decreasing the level of herbivory. These lines are mathematically defined by criteria A5 and A6 (see Appendix) for the water- and nutrient-limitation model, respectively.

Water-limitation model (Fig. 6)

Infiltration rates in sandy soils are higher than in clayey soils. Thus, a high water infiltration in the absence of plants (W_0) corresponds to sandy soils, whereas low water infiltration in the absence of plants corresponds to clayey soils. The rate at which water infiltration increases with plant density (k_2), can be interpreted as the capacity of vegetation communities to improve the structural and water-holding capacities of the soil. As an example, a community of perennial grasses is more capable of improving infiltration rates (low k_2) than communities of annual grasses (high k_2) (Kelly and Walker 1976).

When the soil is clayey (low W_0), a trajectory through the parameter plane while increasing or decreasing the level of herbivory will usually move through the bifurcation set for large ranges of herbivory. When the soil is sandy (high W_0), such a

tween equilibrium plant density P_{eq} and the level of herbivory can be obtained by setting $dW/dt = 0$ and $dN/dt = 0$ in case of water- and nutrient-limitation respectively. This function, as shown in Fig. 3, is called a catastrophe fold (Jones 1977). The point where the plant population will suddenly collapse can be obtained by simultaneously satisfying the analytical criterion $dW_{eq}/dP = 0$ in case of the water-limitation model, and $dN_{eq}/dP = 0$ in case of the nutrient-limitation model. We derived the corresponding solutions of these criteria numerically, as this was analytically not possible.

Catastrophe manifold

A folded surface in three dimensions is shown if the shape of the function depicted in Fig. 3 is related to the parameters W_0 and $r_{N,max}$ in case of the water- and nutrient-limitation model (Figs 4 and 5, respectively). We can now map the five functional states (Fig. 2) on the horizontal parameter planes in a graphical way. The
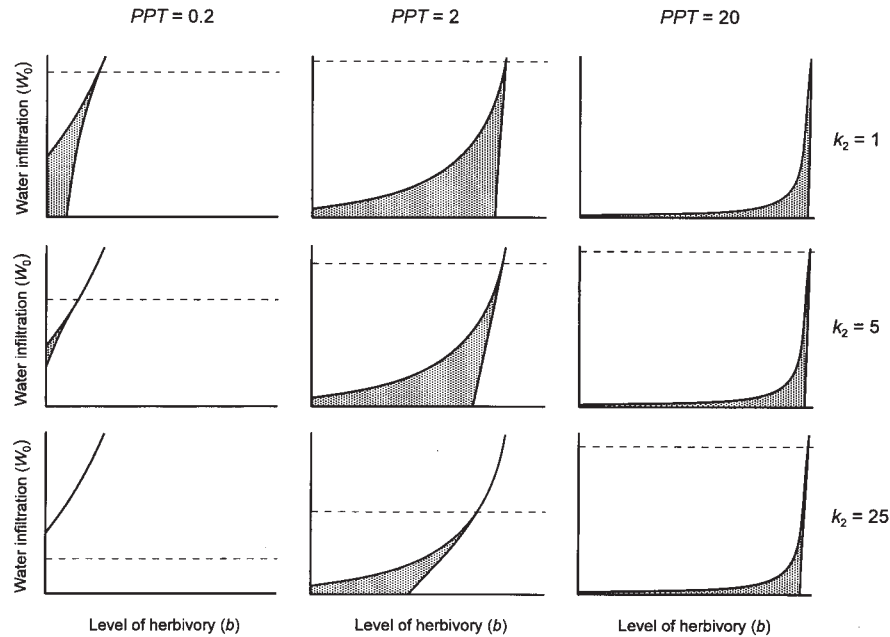
Fig. 6. Bifurcation sets in the parameter planes showing the effect of parameter variations on the qualitative dynamical behaviour of the model systems. The horizontal dashed lines indicate for which parameter combinations a trajectory through the parameter plane will move through the bifurcation set while increasing or decreasing the level of herbivory. Symbols as in Table 1. The functional states are mapped out on the $W_0 - b$ parameter plane for different values of PPT and k_2. Parameter values: $g_{max} = 0.5$, $k_1 = 3$, $d = 0.1$, $c_{max} = 0.05$, $r_W = 0.1$.

trajectory will usually not move through the bifurcation set, or only for small ranges of herbivory. Herbivory is likely to trigger discontinuous and irreversible vegetation changes on soils with a low infiltration capacity. So, on clayey soils, the vegetation will be neither resilient to herbivore impact nor to disturbances, the latter for certain ranges of herbivory.

Fluctuating rainfall may also trigger discontinuous and irreversible changes in plant density if the water infiltration in the absence of plants is relatively low (when the soil is clayey). So, under these conditions, the vegetation will not be resilient to fluctuating rainfall too (which is characteristic for most semi-arid regions). It is more likely that discontinuous and irreversible vegetation changes occur in an environment with fluctuating rainfall than in a relatively stable environment. Even at high rainfall, the vegetation is always overgrazed or stably degraded at a certain fixed value of herbivory, if $b > g_{max} - d$.

When the water infiltration in the absence of plants decreases (when the soil becomes more clayey), the level of herbivory where undergrazed vegetation states change in overgrazed states or alternate vegetation states becomes increasingly lower. If the infiltration capacity of the soil is small and rainfall is low, alternate stable states or "overgrazing" may already occur in the absence of herbivores. This means that it is unlikely that a continuous plant cover can persist, even if herbi-

vores are absent, or that there is no plant production at all because of extremely low soil water levels.

If the capacity of vegetation communities to improve the structural and water-holding capacities of the soil decreases (increasing k_2) the range of herbivory for which alternate stable states are possible becomes smaller, or even disappears if the soil is sandy (high W_0). For more sandy soils, this means that at a certain level of herbivory the overgrazed state may be reached, instead of the alternate stable states situation. For more clayey soils, this means that the system will be stably degraded for lower levels of herbivory. So, if the capacity of vegetation communities to improve the structural and water-holding capacities of the soil decreases, it is likely that more sandy soils become resilient to herbivore impact, environmental fluctuations and disturbances. However, for sandy as well as for clayey soils, bare soil will then already prevail for lower levels of herbivory.

Nutrient-limitation model (Fig. 7)

Maximum specific nutrient loss ($r_{N,max}$) can be interpreted as the erodibility of the soil. The term erodibility reflects the fact that different soils erode at different rates, while other factors that affect erosion remain the same. Water and wind erodibility of soils depend on
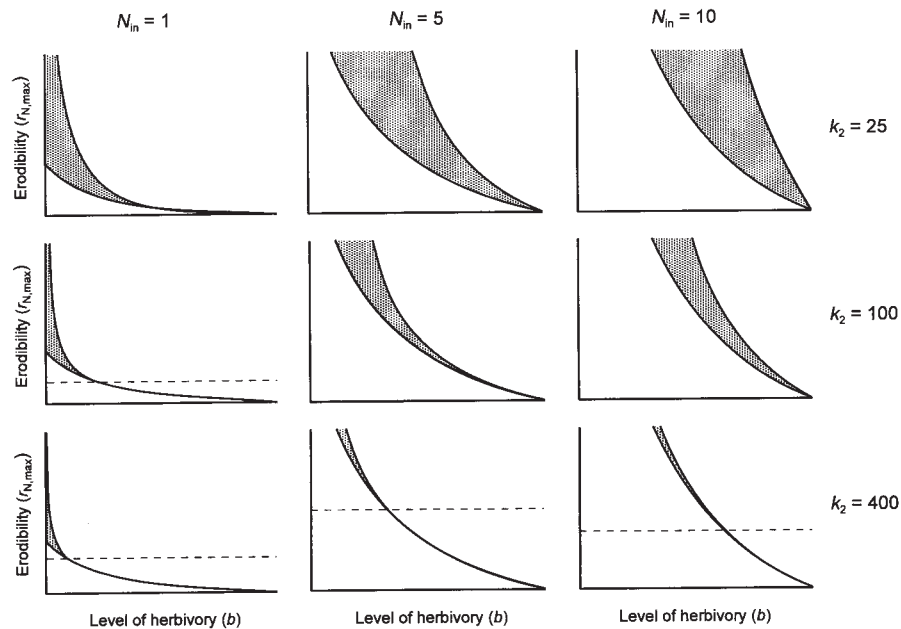
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Fig. 7. The functional states are mapped out on the $r_{N,max} - b$ parameter plane for different values of N_{in} and k_2. Symbols as in Table 1. Parameter values: $g_{max} = 0.5$, $k_1 = 3$, $d = 0.1$, $c_{max} = 0.05$.

aggregate size, aggregate stability and particle size and the value of erodibility increases with an increasing sand content and a decreasing clay content (Bagnold 1973, Evans 1980, Mitchell and Bubenzer 1980). Therefore, a high $r_{N,max}$ corresponds to sandy soils while a low $r_{N,max}$ corresponds to clayey soils. The rate at which specific nutrient loss decreases with plant density (k_2) can be interpreted as the nutrient retention capacity of vegetation communities (cf. Kellman and Sanmugadas 1985).

When the soil is sandy (high $r_{N,max}$), a trajectory through the parameter plane while increasing or decreasing the level of herbivory will usually move through the bifurcation set for large ranges of herbivory. When the soil is clayey (low $r_{N,max}$) such a trajectory will usually not move through the bifurcation set, or only for small ranges of herbivory. Herbivory is likely to trigger discontinuous and irreversible changes in plant density on soils with a high erodibility. So, on sandy soils, the vegetation will be neither resilient to herbivore impact, nor to disturbances, the latter for certain ranges of herbivory.

Fluctuating external nutrient input (N_{in}) may also trigger discontinuous and irreversible changes in plant density for soils with a high erodibility (when the soil is sandy). So, under these conditions, the vegetation will not be resilient to fluctuations in the geochemical cycle too. It is more likely that discontinuous and irreversible vegetation changes occur in a fluctuating environment than in a relatively stable environment. Even at high external nutrient input, the vegetation is always overgrazed or stably degraded at a certain fixed value of herbivory, if $b > g_{max} - d$.

The level of herbivory at which undergrazed vegetation states change in overgrazed states or alternate vegetation states becomes increasingly higher when the erodibility of the soil decreases (when the soil becomes more clayey). If this parameter is high, however, and the external nutrient input is low, alternate stable states or "overgrazing" may already occur in the absence of herbivores. This means that it is unlikely that a continuous plant cover can persist, even if herbivores are absent, or that there is no plant production at all because of extremely low soil nutrient levels.

If the nutrient retention capacity of vegetation communities decreases (increasing k_2) the range of herbivory for which alternate stable states are possible becomes smaller, or even disappears if the soil is clayey (low $r_{N,max}$). For more clayey soils, this means that at a certain level of herbivory the overgrazed state may be reached, instead of the alternate stable state situation. For more sandy soils, this means that the system will be stably degraded for lower levels of herbivory. So, if the nutrient retention capacity of vegetation communities decreases, it is likely that more clayey soils become resilient to herbivore impact, environmental fluctuations and disturbances. However, for clayey as well as for sandy soils, bare soil will then already prevail for lower levels of herbivory.

Discussion

We investigated which prevailing ecological site conditions may lead to discontinuous and irreversible vegetation changes in semi-arid grazing systems. Sandy soils are more vulnerable to nutrient loss through erosion than clayey soils. The model predicts that if plant growth is nutrient-limited, then the vegetation supported by sandy soils is generally less resilient to herbivore impact and fluctuations in external nutrient input, than the vegetation on clayey soils. This depends on the nutrient retention capacity of vegetation communities. Sandy soils have higher infiltration rates than clayey soils. On the other hand, if available soil water limits plant growth, then the vegetation supported by sandy soils is generally more resilient to herbivore impact and rainfall fluctuations, than the vegetation on clayey soils. This, in turn, depends on the capacity of vegetation communities to improve the structural and water-holding capacities of the soil.

Our model provides a general theory which could be applied to areas such as the Sahel, the semi-arid transition zone between the Sahara desert and the Sudanese savannas of West and Central Africa. At the southern border of the Sahel, the mean annual rainfall is 600 mm and at the northern border 100 mm. Water limits growth at the border of the Sahara. This changes to growth limited by nutrients with increasing rainfall to the south. Both sandy soils with eolian origin and soils with loam or loamy–clayey texture are present (Breman and De Wit 1983).

The model predicts that, close to the Sahara, the vegetation supported by sandy eolian soils should be generally resilient to the impact of grazing by livestock and rainfall fluctuations because these soils absorb rainwater well and homogeneously. A continuous vegetation cover could develop if rainfall is sufficient and grazing pressure low. On loamy or clayey soils, crust formation and deterioration of soil structure could occur because of decreasing soil cover and herbivore trampling. Therefore, we expect that the vegetation supported by these soils should be less resilient to grazing impact and rainfall fluctuations. It is rather unlikely that a continuous vegetation cover would persist even if grazing pressure is low, because of low soil water levels. When going further south, away from the Sahara, mean annual rainfall increases and a continuous vegetation cover could persist even if grazing pressure is relatively high. However, rainfall fluctuations, such as the occurrence of a drought, might cause the vegetation supported by loamy or clayey soils to collapse irreversibly if grazing pressure is not rapidly and dramatically decreased by destocking. Water conservation measures might then be needed to carry soil water availability and vegetation biomass above certain breakpoint levels.

Close to the Sudanese savanna, the model predicts that the vegetation supported by sandy soils should generally be less resilient to grazing impact and fluctuations in soil fertility because these soils are easily eroded by water and wind. If the soil is very poor, it is rather unlikely that a continuous vegetation cover would persist, even when grazing pressure is low. Loamy or clayey soils are generally less erodible, therefore we expect that the vegetation supported by these soils should be more resilient to the impact of grazing and fluctuations in soil fertility. A continuous vegetation cover could develop if grazing pressure is relatively low. When grazing pressure is relatively high, a continuous vegetation cover could develop on both soil types, but only if the soil is relatively fertile. On more sandy soils, however, a decrease in external nutrient input might trigger an irreversible vegetation collapse if grazing pressure is not rapidly and drastically decreased. Soil conservation measures might then be needed to carry soil nutrient availability and vegetation biomass above certain breakpoint levels.

Obviously, clayey and sandy soils do not only differ in water infiltration and erodibility. There are also differences in soil nutrient status stemming from parent material and geological processes. In general, clayey soils are more fertile than sandy soils (Penning de Vries and Djitèye 1982). The nutrient properties of both soils are captured in the model by a separate parameter indicating the nutrient release from the geochemical cycle (N_{in}). This makes it possible to study the effects of differences in soil fertility on the dynamics of the system, independent of soil type.

The model predictions are consistent with field observations documented in the literature. Kelly and Walker (1976) found that in areas with heavy textured (clayey) soils, where plant growth was water limited, an increased level of herbivory resulted in a larger proportion of bare soil. Infiltration was about ten times greater under a vegetation cover than through a bare soil surface. We demonstrated that under these conditions vegetation changes driven by grazing or rainfall fluctuations are likely to be found not resilient. Barnes (1965: 106) observed that on a site with deep sandy soils "the ... sandveld remains ... unchanged under very heavy grazing for periods of at least fifteen years". Although this is a rather vague observation, it suggests at least that the vegetation was resistant to herbivore impact. This may be due to the fact that these soils have a high infiltration capacity. We showed that under these conditions vegetation changes are likely to be found resilient.

Abel (1992) concluded that the processes of land degradation are not in all cases the same; in some cases loss of nutrients is important and in other cases decrease in infiltration. He further argued that the relationship between runoff or soil loss and plant cover differs between sites and that this has important implications for management. Abel's (1992) review did not reveal, however, how these relations changed with site-

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specific properties directly relevant to the resilience of vegetation changes and under what conditions loss of nutrients and decrease in infiltration were important. Direct experimental evidence from semi-arid grazing systems to test our theory is non-existent. This is probably due to the inadequacy of our current knowledge to distinguish between reversible and irreversible vegetation changes (Friedel 1991, Laycock 1991, Rietkerk et al. 1996, Rietkerk and Van de Koppel 1997).

The mechanisms responsible for the discontinuous properties of our models are the interactive processes between water infiltration or nutrient loss and plant density. There are other mechanisms which may theoretically lead to similar properties of semi-arid grazing systems, such as the functional response of herbivores to changes in forage availability (Noy-Meir 1975), plant competition for water (Walker et al. 1981), and positive feedback between the occurrence of fire and the presence of certain plant groups (Dublin et al. 1990). But a vast body of literature exists (e.g. Kelly and Walker 1976, Breman and De Wit 1983, Sinclair and Fryxell 1985, Le Houérou 1989, Rietkerk et al. 1996) indicating that plant-soil relations are more important.

The continuous and discontinuous properties of semi-arid grazing systems can be described by applying the cusp catastrophe model (Lockwood and Lockwood 1993, Rietkerk et al. 1996). Unlike the shape of the bifurcation sets derived in this investigation (Figs 6 and 7), the shape of the bifurcation set in the parameter plane of the cusp catastrophe fold is fixed. The present analysis shows that application of the cusp catastrophe model is useful, but only if it aims at illustrating observed catastrophic properties of grazing systems and not when investigating its mechanisms and dynamic implications of these mechanisms.

As Illius and Hodgson (1996: 448) stated, " ... the point of elucidating the concept of resilience is to enlighten the investigation of the biological basis or nature of resilience in grazing systems". We showed that mathematical modelling of system responses to environmental and management inputs provides mechanistic understanding of system properties such as resilience. If this approach is allied to field experimentation, it will provide a strong basis for a functional classification of rangeland types as called for by Stafford Smith (1996).

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Appendix

Analytical analysis of zero-isoclines

We analysed the shape and position of the zero-isoclines for each of the two models. The plant and soil water isoclines for the water-limitation model are respectively:

$$\frac{dP}{dt} = 0 \Rightarrow W^* = \frac{k_1(d+b)}{g_{max} - d - b} \tag{A1}$$

$$\frac{dW}{dt} = 0 \Rightarrow W_{eq} = f(P)$$

where W^* is the amount of soil water for which plant density does not change, and W_{eq} is the equilibrium amount of soil water. The plant and soil nutrient isoclines for the nutrient-limitation model are respectively:

$$\frac{dP}{dt} = 0 \Rightarrow N^* = \frac{k_1(d+b)}{g_{max} - d - b} \tag{A2}$$

$$\frac{dN}{dt} = 0 \Rightarrow N_{eq} = f(P)$$

where N^* is the amount of soil nutrients for which plant density does not change, and N_{eq} is the equilibrium amount of soil nutrients. The soil water isocline W_{eq} and soil nutrient isocline N_{eq} cross the $P = 0$ axis at the points

$$W_s = PPT \frac{W_0}{r_W} \tag{A3}$$

and

$$N_s = \frac{N_{in}}{r_{N,max}} \tag{A4}$$

which are the equilibrium amounts of soil water and soil nutrients, respectively, when plants are absent. These points can be obtained by setting $P = 0$, $dW/dt = 0$ and $dN/dt = 0$ in eqs 2 and 7 and subsequently solving W and N.

The shape of the resource isoclines in the phase plane can be determined from their slopes with respect to P and depend on the effect of the feedback relations 5 and 10 in case of water- and nutrient-limitation, respectively. In case of water-limitation the soil water isocline is a humped-shaped curve whenever

$$\left. \frac{dW_{eq}}{dP} \right|_{P=0} > 0$$

from which can be derived that

$$\left. \frac{dW_{in}(P)}{dP} \right|_{P=0} > c_{max} \frac{W}{W + k_1} \tag{A5}$$

In case of the nutrient-limitation model the soil nutrient isocline is a humped-shaped curve whenever

$$\left. \frac{dN_{eq}}{dP} \right|_{P=0} > 0$$

from which can be derived that

$$\left. -\frac{dr_N(P)}{dP} N \right|_{P=0} > c_{max} \frac{N}{N + k_1} - d \frac{c_{max}}{g_{max}} \tag{A6}$$

In case of the water-limitation model, $W = 0$ is the amount of soil water when plants are present and the limit of instantaneous rainwater uptake is approached. In case of the nutrient-limitation model, $N = k_1 d/(g_{max} - d)$ is the nutrient level where plants are present and the limit of complete nutrient recycling is approached. Despite the quantitative differences between the two resource isoclines, they remain qualitatively identical and can therefore be combined (Fig. 2).

In case of the water-limitation model, the plant isocline crosses the $P = 0$ axis at $W = W^*$. In case of the nutrient-limitation model, the plant isocline crosses the $P = 0$ axis at $N = N^* \cdot W^*$ and N^* are independent of P, so the plant isocline is a straight, vertical line at $W = W^*$ or $N = N^*$ (Fig. 2).