NN08201, 2384

STELLINGEN

I

De catastrofetheorie van de wiskundige Thom is geschikt voor het beschrijven van de vegetatiedynamiek in de Sahel.

Dit proefschrift

II

De discontinue eigenschappen van vegetatiedynamiek in droge graslanden en arctische kwelders kunnen beter worden verklaard door bodemdegradatie dan door een niet-lineaire functionele respons van herbivoren.

Dit proefschrift

III

De waarneming dat één prikkeldraad rond een ranch in de Sahel gedurende de grote droogte van de jaren zeventig het verschil tussen woestijn en weide bepaalde, is voldoende om de toepasbaarheid van de zogenaamde 'nonequilibrium' theorie op droge begrazingssystemen te weerleggen.

Dit proefschrift

IV

Een voortdurende aanleg van waterputten en -pompen voor vee en de toename van het akkerbouwareaal in de Sahel zal het risico van catastrofale vegetatieveranderingen als gevolg van toekomstige droogteperioden vergroten.

Dit proefschrift

V

Het effect van een positive plant-bodem feedback in herbivoor-plant systemen is vergelijkbaar met het Allee-effect in predator-prooi systemen.

Dit proefschrift

VI

Plaatselijke concentraties van Caesalpinioideae boomsoorten met een hoge dichtheid aan individuen, komen niet overeen met de veronderstelde lokaties van laagland-regenbosrefugia in centraal Afrika; deze veronderstellingen dienen derhalve te worden aangepast.

Rietkerk, M., Ketner, P. and De Wilde, J.J.F.E. 1995. Adansonia 17 (1-2): 95-105.

VII

Realisme is geen essentiële eigenschap van een goed model.

VIII

De bescherming van gebieden met hoge natuurwaarde is alleen gegarandeerd zolang het economische meerwaarde heeft.

IX

Intensivering van landbouw in gebieden met onderproductie is een randvoorwaarde voor natuurbehoud.

X

Niet religie maar ideologie leidt tot politiek onderscheid in de huidige Nederlandse democratie; daarom zal het CDA als belangrijke machtsfactor niet terugkeren.

XI
Het door de overheid wijzen op de maatschappelijke verantwoordelijkheid van burgers door middel van televisiespots is overbodig wanneer de overheid haar verantwoordelijkheid neemt en niet effectief wanneer de overheid haar verantwoordelijkheid niet neemt.

XII
Vertrouw op wetenschappers bij het onderkennen van problemen, maar niet bij het verhelpen daarvan.
Ludwig, D., Hilborn, R. and Walters, C. 1993. Science 260: 17, 36.

Stellingen behorende bij het proefschrift
Catastrophic vegetation dynamics and soil degradation in semi-arid grazing systems
van Max Rietkerk

Wageningen, 18 november 1998

Catastrophic vegetation dynamics and soil degradation in semi-arid grazing systems

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Max Rietkerk

Catastrophic vegetation dynamics and soil degradation in semi-arid grazing systems

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
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Abstract

Rietkerk, M. 1998. Catastrophic vegetation dynamics and soil degradation in semi-arid grazing systems. Doctoral thesis; ISBN 90-5485-941-5. Also published in the series Tropical Resource Management Papers No. 20; ISSN 0926-9495, Wageningen Agricultural University, The Netherlands.

The catastrophic properties of the vegetation dynamics of the African Sahel in particular, and of semi-arid grazing systems in general, are revealed. It is proposed that these catastrophic properties are mainly due to soil degradation. Soil degradation can cause a positive feedback between reduced soil water and nutrient availability and reduced vegetation biomass which may lead to collapse of the grazing system. This can be triggered by herbivore impact, especially on loamy or clayey soils in case of water-limited vegetation biomass production, and on sandy soils in case of nutrient-limited vegetation biomass production. In a semi-arid savanna in Tanzania (East Africa) it has been found that a reduction in soil water content and biomass production occurred as a consequence of vegetation litter removal. Hereby, it appeared that increased loss of soil water through increased soil evaporation outbalanced all other effects on soil water content. In a semi-arid grazing system in Burkina Faso (West Africa) it has been found that soil degradation can explain the occurrence and likely persistence of a spatial pattern of vegetated patches alternating with bare soil. Further, it is stressed that catastrophic vegetation shifts leading to desertification in the semi-arid grasslands of the African Sahel as well as in the arctic salt marshes along the Hudson Bay in Canada can both be attributed to positive plant-soil feedbacks.

Key words: catastrophe theory, desertification, patchiness, positive feedbacks, Sahel, thresholds

Acknowledgements

During the period that I worked as a researcher in training, preparing this doctoral thesis, I think that I learned what science is about. I feel that this is my major professional accomplishment during this period, and I hope this doctoral thesis illustrates that accomplishment. My two mentors played a significant role in this but I firstly want to express my deep appreciation to those who provided the personel setting for this accomplishment. The love and friendship of my partner Isabel was, is and will be indispensable for me. The same counts for my parents Kees, Ida and Marja who demonstrated unconditional support. Further, my dear friend Peter demonstrated again and again what friendship is about.

It must have been somewhere at the end of 1993 that Leo Stroosnijder asked me to put my ideas on paper about the phenomenon of threshold effects in the vegetation dynamics of the African Sahel. I clearly remember that he added not to be long-winded and to keep it to one page. At the time, I worked as a research assistant with the group of Herbert Prins, who advised me strongly to take a close look at catastrophe theory. What started with one page ultimately led to this thesis.

Leo, I got this possibility to work on my doctorate thesis thanks to you. You always kept supporting and facilitating my work, no matter my sometimes odd ideas. Herbert, your valuable and indispensable contribution throughout this period was very much appreciated. I remember your instruction of vital importance to keep thinking from behind my computer, while I was about to run away from there, into the field, to start my measurements. I really think that I was very lucky to have you both as my mentors.

I am very glad to acknowledge the valuable and indispensable contributions from other people too. Johan van de Koppel put me on the track of mathematical modelling. I want to thank him for his enthousiastic support in solving mathematical problems and for clarifying discussions, for instance about the similarities between tropical semi-arid grasslands and arctic salt marshes. Frank van den Bosch taught me the beautiful art of biomathematics during his course from which I greatly benefitted. It appeared that he can still find creative solutions if the maths get real complicated. Pieter Ketner shared his knowledge about vegetation with me, and he always found time for lengthy and helpful discussions. I want to thank him for his excellent contributions, especially during the challenging fieldwork in Burkina Faso. Joep Burger and Bart Hoorens also contributed essentially to this fieldwork. During this time, when they were undergraduate students, they showed convincingly that they have the skills and intellect to become good scientists. Claudius van de Vijver kindly invited me to Tanzania where he and Margje Voeten built a fully equipped research camp in Tarangire National Park, from which I benefitted immodestly. He shared his deep insight in the ecology of tropical savannas with me and he demonstrated an impressive perseverance carrying out fieldwork under extreme conditions. Han Olff let me repeatedly pick his statistical brain while keeping his patience. I appreciate him for his talent of making complicated things real simple, which is refreshing in a world where simple things are often made real complicated.

I am pleased to thank here again Jelte van Andel, Jan Bakker, Roy Behnke, Ruben Blijdorp, Henk Breman, Marion Cambridge, Rudi Drent, Margaret Friedel, John Fryxell, Jan van Groenendael, Ignas Heitkonig, Jef Huisman, Andrew Illius, Bob Jefferies, Paul Koene, Hans de Kroon, Manja Kwak, Eddy van der Maarel, Charu Mishra, Marten Scheffer, Diane Srivastava, Mark Stafford Smith, David Tongway and Franjo Weissing, who all contributed directly or indirectly to the improvement of one or more chapters in this thesis. Rob de Boer and Alfred Stein developed very useful software and provided guidance whenever necessary. Peter Buurman, Jessi de Coninck, Paul Kiepe, Fred de Klerk, Tjakkie van der Laan, Abdoulaye Mando, Edward Mielke, Tom Pape, Maja Slingerland, and all staff of Antenne Sahélienne, Chatu Research Camp and Oliver's Camp Ltd. are acknowledged for their friendly support in the lab or in the field. Rob van Genderen provided excellent daily library assistence, and Henk Jochems was always there when he was needed to solve problems with computers or software.

I had the pleasure to share the working environment with respected colleagues from the Erosion and Soil and Water Conservation Group and the Tropical Nature Conservation and Vertebrate Ecology Group of the Department of Environmental Sciences from Wageningen Agricultural University. I shared my office with great pleasure with Fidèle Hien, Abdoulaye Mando, Arnold Sikking and Mehretab Tesfai. They could only stand my company during a few months, after which they fled abroad. I really appreciated their company, patience and humor.

I wrote this doctoral thesis out of appreciation of our natural environment and out of respect for its users. At the same time, the misuse and consequent degradation of our natural environment concern me, as this affects human happiness and even human survival. Therefore, if this thesis contributes to the scientific debate about the consequences of use and misuse of our natural resources in semi-arid grazing systems, from which development policies are derived, this would be very useful indeed.

Max Rietkerk

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Chapter 1

General introduction

Catastrophic dynamics

Can a straw break a camel's back? At first sight, this seems an unreasonable question. But it's not. Of course, it would be naïve to assume that solely a single straw can cause the fracture of the backbone of a camel. But the straw could be the trigger of the event if, for example, the backbone was already weakened by a combination of other factors, such as a heavy load and aging. At the same time, only the removal of that straw from the back of the camel after it is broken, will obviously not lead to the recovery of the fracture, although the original conditions of before the event are perfectly restored. This is exactly what Thom (1975) had in mind when formulating catastrophe theory. Catastrophe theory is a mathematical theory of discontinuous equilibrium changes of a certain state variable as a consequence of continuous changes of one or more control variables. With a simple set of formulas it elegantly describes a whole set of non-linear properties of dynamical systems, also exhibited by ecological systems (Jones 1977), from which the African Sahel is an illustrative example.

The African Sahel is the vegetation transition zone between the Sahara desert and the Sudanian savanna. Here, livestock numbers, including cattle, sheep and goats, have continuously increased from 40 million to over 125 million between 1950 and 1993. This caused marked changes in the vegetation during years of drought in the seventies. In extreme cases, the vegetation dominated by perennial grasses completely collapsed, leading to a greater exposure of bare soil and increased soil erosion by run-off and wind. This was unforeseen by scientists and a catastrophe for the millions of people depending for their subsistence on local pastoral economies. Subsequent removal of livestock from degraded areas, or the occurrence of a succession of relatively wet years after the drought rarely enabled the vegetation to revert to it's former biomass and vegetation composition within a reasonable period of time (several years) (Breman and De Wit 1983, Sinclair and Fryxell 1985, Le Houérou 1989, Schlesinger et al. 1990). Although it would be rash to only attribute this catastrophic vegetation change to excessive grazing pressure (Mace 1991), a simple barbed-wire fence around a 100,000 ha ranch in the Sahel at the time of the years of drought was enough to make a difference between pasture and desert (Wade 1974).

Problem definition

The term semi-arid grazing systems in the title and throughout this thesis is used to characterize environments with an extended dry season, where yearly potential evapotranspiration exceeds yearly rainfall (which is normally highly variable), and where extensive grazing by livestock is the principal type of land use. It is currently firmly believed that vegetation dynamics in these highly variable environments are mainly determined by rainfall, and not by grazing (Ellis and Swift 1988, Tucker et al. 1991, Behnke et al. 1993). Although I would not dare to dispute the overriding importance of rainfall for vegetation dynamics in these systems, I think that this is not the whole story. If it was, this would imply that when vegetation is drastically reduced as a result of episodic intense grazing during drought, it will nevertheless simply recover to it's former biomass and composition if periods with normal rainfall follow. This would completely disregard the possibility of catastrophic vegetation dynamics as described above for the Sahelian example, which is illustrative for semi-arid grazing systems across Africa, Australia (Friedel 1991) and North America (Schlesinger et al. 1990, Laycock 1991). Furthermore, the fact alone that only a simple barbed-wire fence (i.e. grazing) can make a difference between pasture and desert, under the same climatic conditions (Wade 1974), already invalidates this current belief. It is within this context that there is an urgent need to provide an effective explanation of the catastrophic properties of semi-arid grazing systems. This is the main aim of this thesis.

From the simple mathematical models developed by Noy-Meir (1975) and reviewed by May (1977), it became clear that a discontinuous vegetation collapse could be imminent if a grazing system is pushed towards some threshold stocking rate. The analogy with catastrophe theory and observed vegetation dynamics in the Sahel region forced itself upon me. The models of Noy-Meir (1975) further explained that catastrophic vegetation dynamics may occur because of herbivore feeding characteristics. However, a vast body of literature exists on the observed relationship between high levels of grazing and soil degradation, i.e. soil erosion by run-off and wind, and the consequent loss of water and nutrients (Elwell and Stocking 1976, Breman and De Wit 1983, Sinclair and Fryxell 1985, Schlesinger et al. 1990). This might provide a more effective explanation of catastrophic vegetation dynamics than herbivore feeding characteristics, especially for grazing systems under semi-arid conditions, as it is under these conditions that the availability of water and nutrients limits vegetation production (Breman and De Wit 1983). In this thesis I focus on the following research question: what are the dominant mechanisms causing catastrophic vegetation changes in semi-arid grazing systems and under which conditions do they occur? My initial hypothesis was that soil degradation might lead to an alternative explanation of catastrophic vegetation dynamics in semi-arid grazing systems.

Methods

We use catastrophe theory to describe the anology with the vegetation dynamics of the African Sahel. In general, if one suspects a certain system to behave catastrophically, catastrophe theory can be used as a tool to deduce hypotheses about the conditions under which such catastrophic dynamics may be expected. Because it is a descriptive tool in the sense that such an exercise is a *post hoc* interpretation of observed dynamics, an important drawback of catastrophe theory is that it does not provide any insights in the underlying mechanisms of catastrophic behaviour. For that, the following tool is appropriate.

This is the tool of "minimal" models. We use minimal models to unravel cause and effect of catastrophic dynamics. This type of models is particularly useful in enhancing the insight in mechanisms explaining phenomena observed in nature (Scheffer and Beets 1994). Minimal models typically focus on specific mechanisms, leaving out many beautiful ecological details, like the classic models of Noy-Meir (1975). Actually, this type of models can be best characterized as thought experiments. Analogous to laboratory or field experiments, the central idea is to standardize conditions, and not to capture the realism of the whole ecosystem, so that the effect of a specific factor is thrown into relief against a constant background.

Last but not least, field experiments were performed to test hypotheses generated by the minimal models. A specific tool that we used when analysing the data obtained from field experiments is geostatistics. The main difference between statistics and geostatistics is that in geostatistics variables are linked to locations. Such variables are termed "regionalized" variables. The geostatistical toolbox was designed to quantify the phenomenon of spatial (in)dependence of regionalized variables (Isaaks and Srivastava 1989). For example, geostatistics are indispensable for analysing the degree and scale of spatial variation, and for comparing spatial patterns. In this study, we use geostatistics to analyse spatial (in)dependence of selected regionalized vegetation and soil variables along a gradient of herbivore impact.

Outline of the thesis

This thesis brings together a number of coherent papers on catastrophic vegetation dynamics and soil degradation in semi-arid grazing systems. Chapter 2 is an interpretation of Sahelian vegetation dynamics in terms of catastrophe theory. This chapter mainly serves as a description of catastrophic properties of these dynamics, also exhibited by catastrophe theory. In Chapter 3, we focus on the interactions between water infiltration or nutrient retention and vegetation biomass, two crucial plant-soil feedbacks generally operating in semi-arid grazing systems, to analyse their implications for system dynamics. In Chapter 4, we further elaborate on the models of the former chapter, with the aim to predict under which site-specific conditions vegetation changes as a consequence of grazing could be irreversable. Here, we explicitely stress the applicability of the models to the Sahel environment.

Feedback relations between aboveground vegetation biomass and soil water content were experimentally investigated in a semi-arid savanna in Tanzania; the results are described in Chapter 5. Here, we focus on the question how the removal of aboveground biomass, including litter and perennial grass tufts, affects the soil water balance and how this subsequently affects tuft production. In Chapter 6, we study vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in Burkina Faso, to investigate the spatial implications of operating plant-soil feedbacks. In Chapter 7, we stress the general applicability of the insights derived from our studies, in comparing catastrophic vegetation dynamics in semi-arid grasslands and arctic salt marshes. Finally, I discuss the results in general terms in Chapter 8 and I provide ideas for future research. In this chapter, I also relax some assumptions of our original models regarding herbivore functional responses and herbivore population regulation in order to investigate the implications for system dynamics.

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Chapter 2

Sahelian rangeland development; a catastrophe?

Max Rietkerk, Pieter Ketner, Leo Stroosnijder and Herbert H.T. Prins

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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 five 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.

Introduction

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 could 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 five 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.

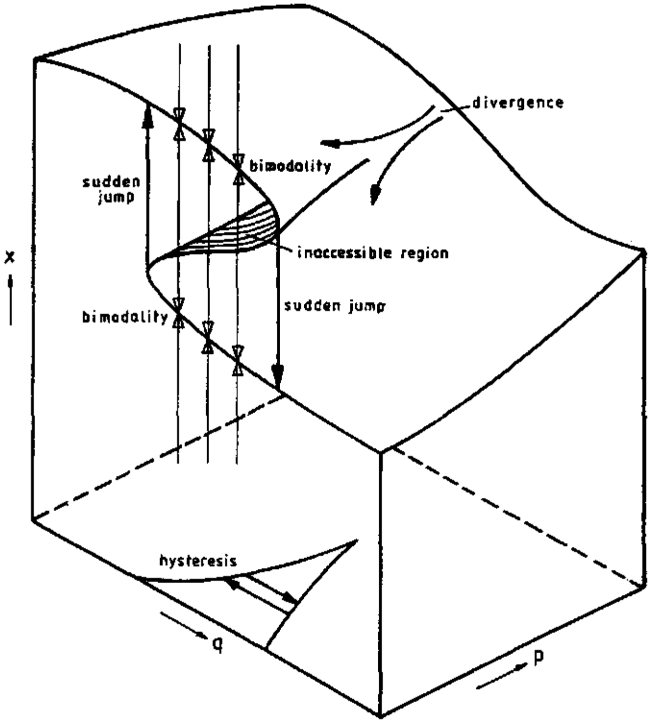

Fig. 1. The cusp catastrophe manifold with five catastrophe flags (Gilmore 1981, Lockwood and Lockwood 1993). These flags occur if the values of the control variables are within the bifurcation set, indicated by the cusp-shaped line on the horizontal control surface. The state variable is represented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

The 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, 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 these 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).

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 run-off 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.

The herb layer of the Sahelian rangelands can be divided into three 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 one or two 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 two 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. Fig. 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.

Box 1. Division of the herb layer of the Sahelian rangelands into three 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

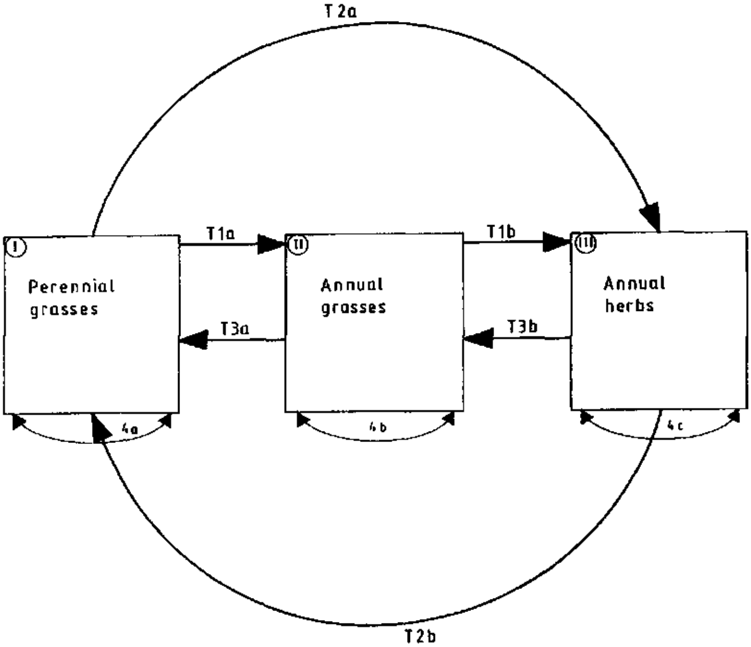

Fig. 2. A state-and-transition diagram for the herbaceous vegetation dynamics of Sahelian rangelands based on Breman et al. (1980) and Cissé (1986). The state-and-transition formulation has been taken from Westoby et al. (1989). Catalogues in Box 2.

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.

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 three 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. Fig. 3 illustrates the proposed configuration of state and control variables along the axes of the cusp catastrophe model.

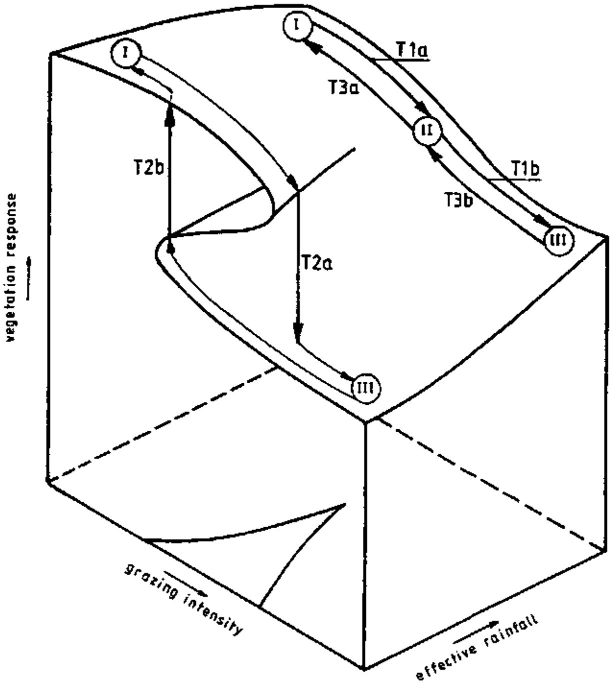

Fig. 3. The cusp catastrophe model applied to Sahelian rangeland dynamics. The vectors along the cusp manifold are the transitions as indicated in Fig. 2 and Box 2.

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 three 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 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 five 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).

Bimodality

Bimodality means that an ecosystem has two 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 the 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 one 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.

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).

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 (Figs 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. That 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 through trampling. 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.

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 one or two 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.

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 two 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 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 two 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 five so-called catastrophe flags will only occur when the values of the control variables are *within* the bifurcation set. There are, however, three 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 one 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 (refering 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 (1997) (Chapter 3 in this thesis) 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:

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

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:

$$V'(x) = x^3 + px + q = 0 \qquad \text{A1}$$

The bifurcation set is the subset of equation A1 for which the following equation is also satisfied:

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

In Fig. 4 the potential functions $V(x)$ are presented for three 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.

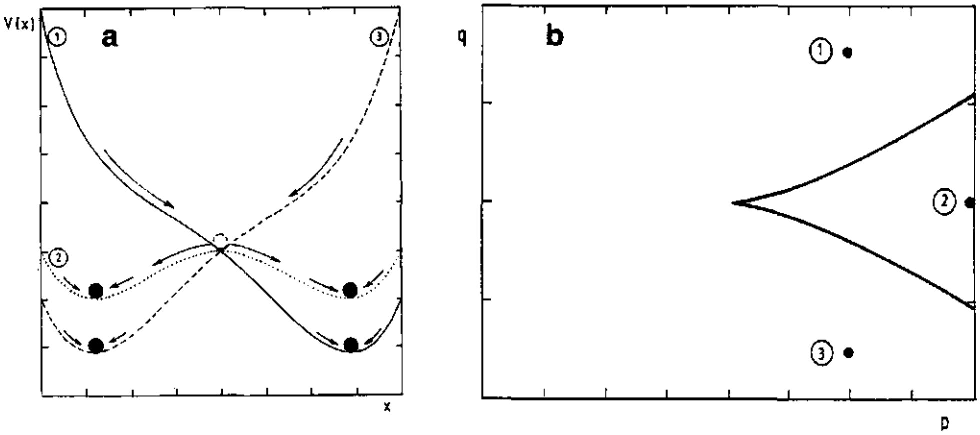

Fig. 4. (a) The curves of the potential function $V(x)$ for three different pairs of values of the control parameters p and q. The three different pairs of values of the control variables are indicated by the numbers 1, 2 and 3. The light circle with the diverging arrows represents the location of an 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.

Chapter 3

Alternate stable states and threshold effects in semi-arid grazing systems

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Abstract

Models that explain the discontinuous behaviour of semi-arid grazing systems usually emphasize herbivore feeding characteristics or plant competition as possible mechanisms. Field studies indicate, however, that plant-soil relations could be more important. We show by means of a graphical model that the interactions between water infiltration or nutrient retention and plant density potentially give rise to the existence of alternate stable vegetation states and threshold effects in semi-arid grazing systems, even without the effect of a non-linear herbivore functional response or plant competition. These interactions may trigger a positive feedback between reduced plant density and reduced resource availability, and lead to a collapse of the system. The model results are in line with well-documented observations of spatial and temporal patterns such as two-phase mosaics and stably degraded grasslands.

Introduction

Theoretical and empirical evidence for the existence of alternate vegetation states and threshold effects in grazing systems were presented two decades ago (Noy-Meir 1975). Alternate states may occur if at low plant density plant losses due to herbivory exceed plant growth, while at high density the reverse is true [see May (1977) for a review]. The shapes of the herbivore consumption functions (functional responses) and plant growth functions play a central role in Noy-Meir's models, but the models do not address the underlying mechanisms of low plant growth rates at low plant density.

A vast body of literature exists on the relationship between high levels of herbivory and soil degradation (Elwell and Stocking 1974, Kelly and Walker 1976, Breman and De Wit 1983, Sinclair and Fryxell 1985, Le Houérou 1989, Prins 1989) which might contribute to a mechanistic explanation. A reduction of plant density often leads to a higher amount of rainfall running off instead of infiltrating into the soil and, because of that and wind erosion, to higher nutrient loss. The influence of vegetation on the infiltration rate of water into the soil and the rate of nutrient loss is more pronounced at the lower end of the plant density continuum than at the higher end (Walker et al. 1981, Stocking 1994). Plant growth will be affected by these processes, especially in semi-arid regions where growth is mainly governed by nutrient and water availability (Walker et al. 1981, Penning de Vries and Djitèye 1982, Breman and De Wit 1983). Hence, at low plant density, plant growth could be reduced below grazing induced plant losses, thereby adversely affecting the stability of semi-arid grazing systems.

In this paper we consider the main plant-soil relations occuring in semi-arid grazing systems and we investigate how they may influence the dynamics of these ecosystems by analysing a simple graphical model. The model provides a new and conceptually effective explanation of the properties of these discontinuously stable grazing systems.

Model grazing system

Assumptions

A characteristic feature of semi-arid grasslands is that either water or nutrients limit plant growth (Penning de Vries and Djitèye 1982, Breman and De Wit 1983). In a water-limited system, plant growth is assumed to be determined only by water availability. In this case, we assume a constant rainfall and a constant proportion of soil water lost from the system per unit of time, through evaporation and percolation. In a nutrient-limited system, when plant growth is determined solely by nutrient availability, we assume a constant amount of nutrient released from the geochemical cycle per unit of time. For the sake of simplicity, a constant fraction of plant losses due to mortality (not grazing-induced) is assumed to be shunted directly into the soil nutrient pool and is subsequently available for plant growth (cf. DeAngelis 1992). The level of herbivory is kept constant, which is a good approximation to management practices in grazing systems (Noy-Meir 1975). A linear functional response of the herbivore to changes in forage availability is assumed, although we acknowledge that a saturating, sigmoid or hump-shaped response may be more realistic (Crawley 1983, Fryxell 1991, Van de Koppel et al. 1996). However, the effects of the plant-soil interactions on plant density are central in our investigation and not the shape of the functional response. The model we derive does not intend to capture the entire system but examines the consequences of dominant plant-soil interactions for the dynamics of the system. The model systems are mathematically defined in the Appendix.

Zero-isoclines of plants and resources

A simple way to analyse the dynamics of these water- and nutrient-limitation models is by plotting the zero-isoclines of the plant and its resources in a phase plane (e.g. Edelstein-Keshet 1988) (Fig. 1). The plant isocline is the line joining combinations of plant density and soil water or nutrients along which plant density does not change. We assume that plant production requires a certain minimum amount of soil water in case of water-limitation, or nutrients in case of nutrient-limitation, independent of plant density (see Armstrong and McGeehee 1980, Tilman 1982 for further details). Hence, the plant isocline is a straight, vertical line. At higher levels of soil water or nutrients, plant production is positive, while at lower levels plant production is negative. If the level of herbivory increases, the critical demand for soil water or nutrients increases and the plant isocline shifts to the right. Plant growth has to compensate for the increased level of herbivory in order to sustain production.

The soil water isocline is the line joining those combinations of plant density and soil water where the amount of soil water does not change. In the absence of vegetation the uptake rate of water by plants is zero and the soil eventually reaches an equilibrium value for the amount of soil water. Increasing plant density leads to a decreasing amount of soil water at equilibrium because the rate of total water uptake increases. When there is a constant infiltration rate and no run-off, the isocline has a negative slope (see Appendix).

The nutrient isocline is the line joining those combinations of plant density and soil nutrients at which the latter does not change. In absence of vegetation the nutrient uptake rate by the plants is zero and the amount of soil nutrients eventually reaches an equilibrium. With increasing plant density the total rate of nutrient uptake increases. Thus, if a constant proportion of soil nutrients is lost from the system, this isocline has a negative slope too. Note that the shapes of the soil nutrient and soil water isocline are identical (see Appendix). Therefore, we combine the two isoclines; this results in a new isocline which we term "resource isocline" (Fig. 1).

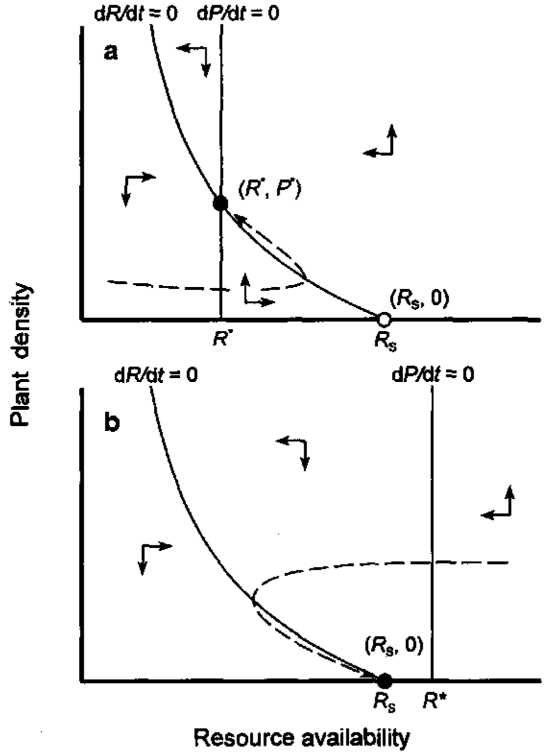

Fig. 1. (a) The zero-isoclines for plant density (dP/dt=0) and resources (dR/dt=0) (soil water or nutrients) illustrated in the phase plane. The zero-isoclines for soil water and nutrients have the same shape and are plotted together. The vectors indicate the direction of change. The dotted line illustrates the path which the system follows during time, given the starting point as indicated. R^* is the minimal amount of resources necessary for plant production. R_s is the equilibrium amount of resources in the absence of plants. The dark circle is a stable equilibrium at (R^*,P^*) and the light circle is an unstable equilibrium at (R_s,0). Note that $R^*<R_s$. (b) At a high level of herbivory, the system is overgrazed and the zero-equilibrium becomes stable because $R^*>R_s$. The system always shifts to the zero-equilibrium, indicated as a dark circle.

Stability without feedbacks

When the plant and resource isoclines are drawn together in one phase plane as in Fig. 1, this results in a graphical representation of a grazed ecosystem with one or two equilibria, depending on the level of herbivory. Let P be plant density, R the amount of resources, R^* the minimal amount necessary for plant production and R_s the equilibrium amount of resources in the absence of plants. At low levels of herbivory, when $R^*<R_s$, two equilibria exist, one unstable boundary equilibrium with no vegetation at (R_s,0), and one stable internal equilibrium at (R^*,P^*) (Fig. 1a and Appendix). The equilibrium at P=0 is unstable; any addition of seed (or any propagule) immediately leads to a further increase in plant density. Thus, for all initial conditions with a positive plant density, the system will move to the internal equilibrium.

An increase of herbivory shifts the plant isocline to the right, which leads to a decrease in equilibrium plant density. At high levels of herbivory, when $R^*>R_s$, there is only one equilibrium, at (R_s,0) (Fig. 1b). Consumption of plants by herbivores exceeds plant production, or, in other words, resource levels are unsufficient for the plant to compensate for herbivore consumption. This causes the boundary equilibrium to be stable (see Appendix); the system is overgrazed.

Plant soil relations

Shape of the relationships

The mechanisms underlying the effect of vegetation on the capacity of the soil to absorb water and retain nutrients can be described by two simple relationships. Vegetation improves the structural and water-holding properties of the soil by forming root channels, by preventing crust formation through the interception of raindrops, and by stimulating biological activity in the soil, resulting in higher infiltration rates (Glover et al. 1962, Kelly and Walker 1976, Van Wijngaarden 1985, Scholte 1989, Kiepe 1995). A particular shape of the relationship between plant density and infiltration rate is proposed by Walker et al. (1981) (Fig. 2a). Empirical evidence for the shape of this relationship can be found in Van Wijngaarden (1985). In the absence of vegetation, there is some infiltration but a large fraction of rainfall is lost as surface run-off. Initially, the rate of infiltration increases rapidly as plant density increases. At the same time, soil cover by plants also increases and the positive effect of increasing density on the infiltration rate is at its maximum when the soil is completely covered by plants. Hence, with increasing plant density the rate of infiltration approaches asymptotically the maximum rate of infiltration, which can not surpass the rainfall rate.

Vegetation protects the soil against wind and water erosion by the physical binding of soil by stems and living roots, raindrop interception, and the retention of run-off (Elwell and Stocking 1974, 1976, Lang 1979, Graetz 1991, Stocking 1994). Consequently, a higher plant density leads to a lower nutrient loss. Based on the results of experiments (Elwell and Stocking 1974, 1976, Lang 1979) and assuming a linear relationship between soil loss and nutrient loss, the form of the relationship between plant density and specific nutrient loss rate can be expressed graphically (Stocking 1994) (Fig. 2b). Where there is no vegetation, the specific nutrient loss rate is maximal. Initially, the specific nutrient loss rate rapidly decreases as density increases. The effect of increasing plant density on the specific nutrient loss rate diminishes at high biomass values. The interactive processes between plants and soil become increasingly effective at coping with erosive processes, hence the specific nutrient loss rate approaches zero with increasing plant density.

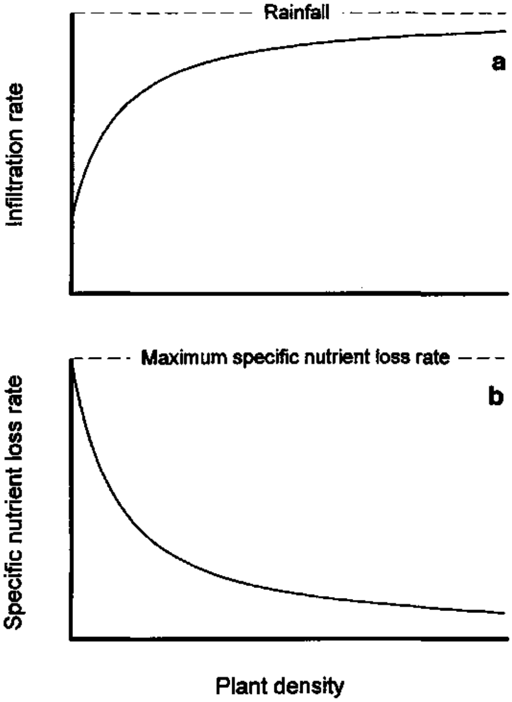

Fig. 2. (a) The shape of the feedback relation between infiltration rate and plant density [after Walker et al. (1981)]. Empirical evidence for the shape of this relationship can be found in Van Wijngaarden (1985). The infiltration rate is defined in relative terms as the amount of water entering the soil expressed as a proportion of the amount which enters when plant density is at its maximum. (b) The shape of the feedback relation between the specific nutrient loss rate and plant density based on the results of experiments by Elwell and Stocking (1974, 1976) and Lang (1979).

Effect of plant-soil relations

If a feedback relation between the rate of infiltration and plant density is incorporated in the water-limitation model, the shape of the soil water isocline in the phase plane alters. At low plant density, any increase in density results in a relatively large increase in the infiltration rate, possibly even exceeding the increase in the rate of water uptake by plants. In this case, the isocline has a positive slope (Fig. 3). Above a certain plant density, however, the effect of increasing plant density on water infiltration declines, and as a result the increase of water uptake by the plants will exceed the increase of water infiltration. Consequently, a hump appears in the soil water isocline (see Appendix). If the feedback relationship between plant density and nutrient loss is incorporated in the nutrient-limitation model, the shape of the nutrient isocline in the phase plane changes likewise. At low plant density, any increase in density results in a relatively large reduction of the specific nutrient loss rate. This results in a nutrient isocline that has a positive slope. Above a certain plant density, however, the decrease in nutrient loss plus the increase in nutrient release from plant mortality becomes lower than the increase in nutrient uptake by the plants. This produces the hump in the nutrient isocline (see Appendix). Again, the shape of the two isoclines are identical, so we can continue the analysis using the general resource isocline (Fig. 3).

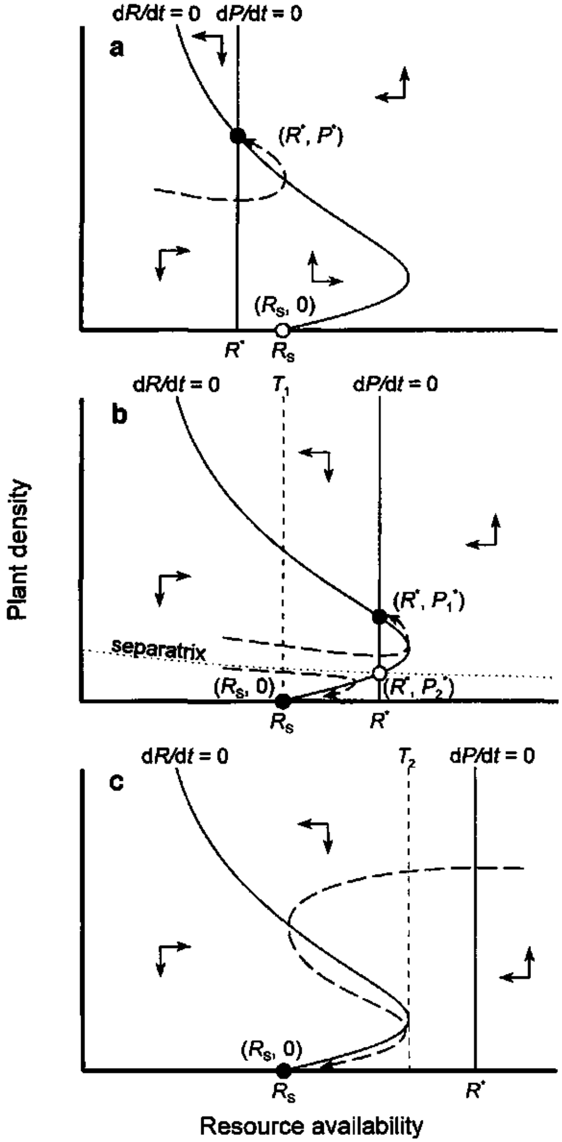

Fig. 3. (a) The humped soil water and nutrient isocline drawn together as one resource (R) isocline in a phase plane. Note that $R^*<R_s$. The light circle indicates an unstable equilibrium and the dark circle a stable one. (b) If the level of herbivory crosses a certain threshold T_1, where $R^*=R_s$, there are three equilibria: a stable one at P=0 (R_s,0) and one at a high plant density (R^*,P_1^*), and an unstable one at a low plant density (R^*,P_2^*). (c) At a level of herbivory higher than the threshold T_2, the system is overgrazed and always shifts to the boundary equilibrium at P=0, independent of initial conditions.

Stability with feedbacks

When the plant and the humped resource isocline are plotted together in one phase plane as in Fig. 3, a graphical representation of a grazing system is obtained, with one, two or three equilibria, depending on the level of herbivory. At low levels of herbivory (if $R^* < R_s$) the system has two equilibria, comparable with a lightly grazed system in which feedbacks are absent (Figs 3a, 1a).

If herbivory is increased, however, a certain threshold (T_1) will be crossed at $R^* = R_s$. There are now three equilibria: a stable one without vegetation (R_s,0), a stable one at high plant density (R^*,P_1^*), and an unstable one at intermediate plant density (R^*,P_2^*) (Fig. 3b) (see Appendix). The two domains with different attracting equilibria that occur in the phase plane are separated by a separatrix (dotted line). For initial values of plant density and resource levels under the separatrix, the system shifts to the equilibrium at $P=0$. For initial values above the separatrix, the system shifts to the equilibrium at high plant density. Under these conditions an environmental fluctuation or disturbance (e.g. fire) may carry the plant density or available resource levels below a breakpoint value (indicated by the separatrix), whereupon the system collapses. Note that both the differences in initial conditions and equilibrium resource levels may be very small and undetectable.

At levels of herbivory higher than the threshold T_2, the system is overgrazed (Fig. 3c). There is only one stable equilibrium, the no-vegetation equilibrium (R_s,0). The consumption rate of the herbivores is so high that the system always shifts to that zero-equilibrium, independent of initial conditions. This situation is comparable with an overgrazed situation without feedbacks (Fig. 1b). However, when the level of herbivory is lowered in the situation where feedbacks do not operate, it leads to a continuous increase of plant density at equilibrium. Lowering herbivory to a level between the thresholds T_1 and T_2 in the situation where feedbacks operate has no effect at all. The system can only be restored if plant density or resource levels are increased dramatically beyond certain breakpoint values. Hence, the system is stably degraded (cf. Prins 1989).

Model robustness

In order to determine the consequences of the assumptions of a linear herbivore functional response and plant growth being limited by resource availability only, we investigated the effect of a non-linear functional response and density dependent plant mortality on the model results. These models exhibit qualitatively similar behaviour. Further, relaxing the assumption that the detritus and available nutrients are one nutrient pool, we investigated the effect of separating the available nutrients N from the detritus D on the model results by an analysis of the isocline surfaces of a three compartment model. Hereby, we assumed that a constant fraction of the plant losses goes to the detrital compartment and a constant decomposition of detritus, releasing the nutrients into the available pool. In case of a negative feedback of detritus loss fraction and plant

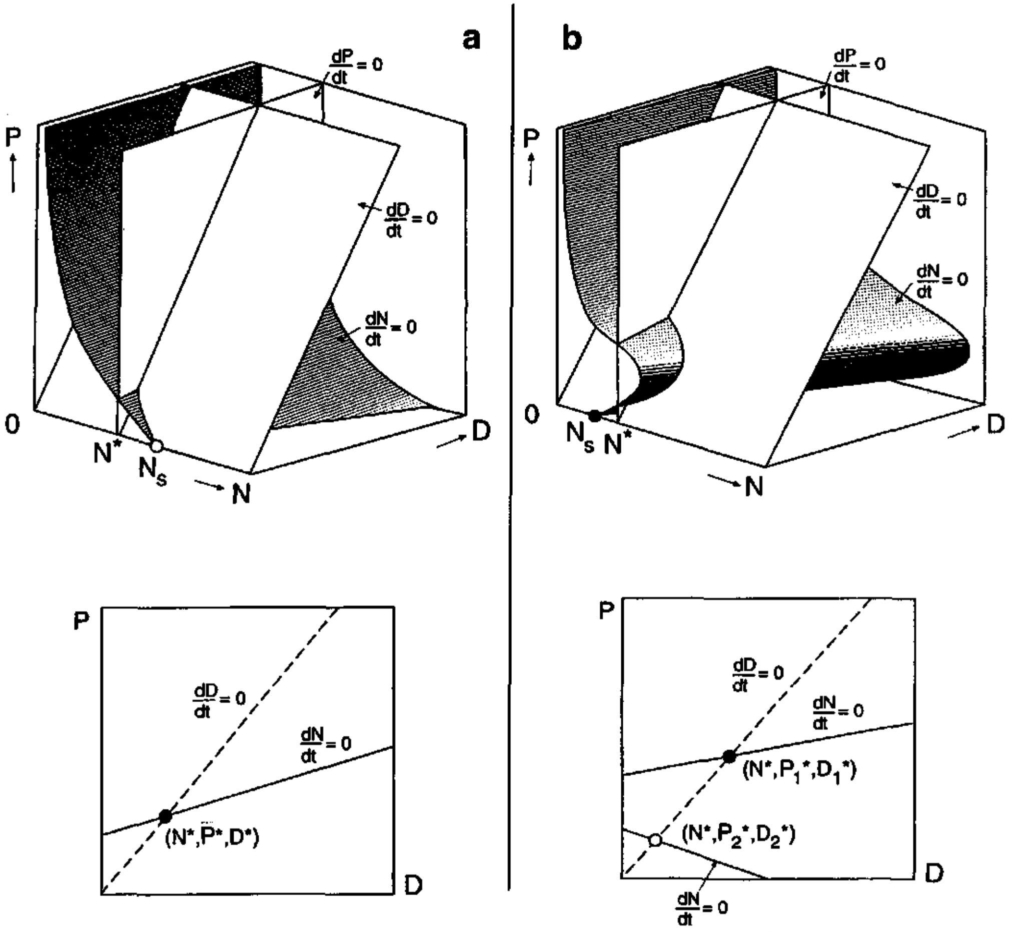

Fig. 4. (a) Isocline surfaces for available nutrients (N), plant density (P) and detritus (D). Note that the intersection of these surfaces is an equilibrium point. If $N^*<N_s$ the system is characterized by two equilibria, one unstable boundary equilibrium with no plants at (N_s,0,0) and one stable internal equilibrium at (N^*,P^*,D^*). This internal equilibrium can be visualized by means of the projection of the intersection lines of the isocline surfaces of the available nutrients and detritus on the detritus-plant density plane (seen from the right side of the cube). If $N^*>N_s$ there is no internal equilibrium and the boundary equilibrium becomes stable. (b) If $N^*>N_s$ the system can be characterized by three equilibria: a stable boundary equilibrium with no vegetation at (N_s,0,0), a stable internal equilibrium at high plant density (N^*,P_1^*,D_1^*), and an unstable internal equilibrium at low plant density (N^*,P_2^*,D_2^*). The internal equilibria can be visualized by the same means as in fig. 4a. If $N^*<N_s$, the boundary equilibrium becomes unstable and the unstable internal equilibrium does not exist.

density (the available nutrient loss fraction being constant), the system is characterized by two equilibria (if $N^* < N_s$), one unstable boundary equilibrium with no plants at (N_s,0,0) and one stable internal equilibrium at (N^*,P^*,D^*) (Fig. 4a). No alternate stable states or threshold effects exist. In case of a negative feedback of available nutrient loss fraction and plant biomass (the detritus loss fraction now being constant), the system can be characterized by three equilibria (if $N^* > N_s$): a stable one with no vegetation at (N_s,0,0) and one at high plant density (N^*,P_1^*,D_1^*), and an unstable one at low plant density (N^*,P_2^*,D_2^*) (Fig. 4b). In this case, evidently, alternate stable states and threshold effects exist because a hump appears in the available nutrient isocline surface.

So, we think that the results derived in this paper are quite robust as all these models show that the interactions between water infiltration or nutrient retention and plant density may trigger a positive feedback between reduced plant density and reduced resource availability, and lead to a collapse of the system.

Discussion

It is recognized that herbivory affects plant growth by altering the supply of resources for the surviving plants (Owen and Wiegert 1976, McNaughton 1979). Several studies stress the importance of nutrients released from dung (Ruess and McNaughton 1984, Hik and Jefferies 1990) or increased mineralisation (Holland and Detling 1990, Holland et al. 1991, Seagle et al. 1992), leading to an increase of plant growth. In this paper, we analysed two relations that cause the opposite, that is, resource levels to drop as a result of herbivory, leading to a reduction of plant growth. These feedback relations potentially give rise to the existence of alternate stable vegetation states and threshold effects in grazed ecosystems even without the effect of a non-linear herbivore functional response (Noy-Meir 1975) or plant competition (Walker et al. 1981).

The results of the model are consistent with well-documented observations of spatial and temporal patterns in grazed ecosystems. Two-phase mosaics (densely vegetated patches regularly alternating with almost bare areas) occur on smooth slopes and even flat landscapes of (semi-)arid lands (Boaler and Hodge 1964, Wickens and Collier 1971, McNaughton 1983, Belsky 1986, Montana 1992, Ludwig and Tongway 1995). Many different composite factors are involved in building and maintaining the two-phase mosaics, e.g.: compaction of the soil by large herbivores, fluvial run-off - run-on, aeolian saltation-deposition and below-ground biological activities. However, the existence of these patterns can probably be best explained in general terms by the positive feedback of water infiltration (cf. Belsky 1986) or nutrient retention (cf. Ludwig and Tongway 1995) and plant density. McNaughton (1983) and Belsky (1986) further found that a two-phase mosaic in the Serengeti disappeared if large herbivores were excluded. This means that, although the differences in water-infiltration rates between the two discrete vegetational phases was in this case the most important factor causing their stable existence, grazing ultimately triggered the discernable changes. Additionally, examples from grazing systems in Africa, North America and Australia, where overgrazing and soil degradation led relatively rapidly to a low (or bare) vegetation state, showed that improvement could not be attained on a practical time scale by simply lowering the level of herbivory (Sinclair and Fryxell 1985, Friedel 1991, Laycock 1991, Daily 1995, Rietkerk et al. 1996, Chapter 2 in this thesis). The degraded grasslands can only be improved if plant density or resource levels are increased dramatically beyond certain breakpoint values by means of human intervention.

The patterns described above do not occur solely in semi-arid grazing systems. Similar vegetation mosaics are reported for arctic coastal plant communities in Canada (Jefferies 1988a,b). While summer grazing by geese, when plant growth is vigorous, results in a grazing lawn of graminoid species, spring grubbing for roots and rhizomes often leads to the destruction of existing plant communities and the creation of "barrens". Lacking vegetation cover, the soil is eroded and becomes hypersaline, resulting in the removal of organic matter and decreasing mineralisation of nitrogen (Srivastava and Jefferies 1996, Wilson and Jefferies 1996). The resulting edaphic environment is unsuitable for the colonization and establishment of the original plant communities, at least over considerable time spans.

Walker et al. (1981) modelled the competition between a woody vegetation and grasses for available soil water in a water-limited system. According to them, this competition, combined with the effects of the herbivore functional response and the positive interaction between grass biomass and infiltration rate, may lead to the development of two alternate stable states in semi-arid savannas: one with much woody vegetation, and one with a relatively large biomass of grass and rather little woody vegetation. We focus on a simpler case by omitting many complicating ecological factors that may occur in real semi-arid systems. Our point could therefore even be further generalized. Any positive plant-soil feedback that is strong enough to create a hump in the resource isocline may cause alternate stable states. Consequently, any factor inducing shifts in the position of the plant isocline (e.g. grazing) or resource isocline (e.g. environmental fluctuations) may trigger threshold effects. As plant-soil interactions serve as one of the most influential positive feedback loops in semi-arid grazing systems (Graetz 1991), we believe that our minimal modelling approach provides insights of general importance.

Further understanding of the behaviour of a system where feedbacks operate between plants and resources will help to establish whether the system may collapse under certain conditions, and whether there are warning signs of an imminent collapse. This is important for the management of pastoral or protected savanna areas.

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Appendix

Analytical justification of the graphical results

We analysed the properties of both two compartment models discussed above using the following condensed model:

$$\frac{dR}{dt} = F(R,P) = R_{in}(P) - c(R)P - r(P)R \qquad \text{A1}$$

$$\frac{dP}{dt} = G(R,P) = g(R)P$$

where $R_{in}(P)$ describes the resource input as a function of plant density P, and $r(P)$ describes the resource losses as a function of P. Both net specific resource uptake by plants $c(R)$ and specific plant growth $g(R)$ are monotonically increasing functions of R. Specific plant growth $g(R)$ equals zero at $R=R^*$.

In case of the water-limitation model, $r(P)$ is constant, while $R_{in}(P)$ is a monotonically increasing function of P (Fig. 2a). $R_{in}(P)$ levels off to the value of $R_{in,max}$ at high values of P. $c(R)$ is assumed to be zero at zero resource availability R, since water does not recycle. In case of the nutrient-limitation model, $R_{in}(P)$ is constant, while $r(P)$ is a monotonically decreasing function of P (Fig. 2b). $r(P)$ levels off to the value of r_{min} at high values of P. $c(R)$ is assumed to be negative at low values of R, due to recycling of plant nutrients, but is positive at resource levels higher than $R=R_u$.

General shape of the resource isocline

The resource isocline intersects with the P=0 axis at the point $R_s=R_{in}(0)/r(0)$. The slope of the isocline at $(R_s,0)$ can be obtained by implicit differentiation of the isocline equation ($dR/dt=0$) with respect to P:

$$\frac{dR}{dP} = -\frac{\frac{\partial F}{\partial P}}{\frac{\partial F}{\partial R}} = -\frac{\frac{dR_{in}(P)}{dP} - c(R) - \frac{dr(P)}{dP}R}{-\frac{dc(R)}{dR}P - r(P)}$$

The sign of dR/dP is determined by the numerator, since the denominator is always negative. So, the criterion for an isocline with a positive slope reads:

$$\frac{dR_{in}(P)}{dP} - \frac{dr(P)}{dP}R > c(R) \qquad \text{A2}$$

In ecological terms, the isocline has a positive slope whenever, with increasing P, the increase of net resource input into the system is higher that the increase in consumption. However, the left-hand side of A2 decreases and approaches zero with increasing P, since $d^2R_{in}(P)/dP^2<0$ and $dr(P)/dP=0$ in case of the water-limited system, or $d^2r(P)/dP^2>0$ and $dR_{in}(P)/dP=0$ in case of the nutrient-limited system. As $dc(R)/dP=0$, it follows that dR/dP will drop and become negative, resulting in an isocline that has a negative slope at high values of P. Thus, for both models we expect an isocline that has a positive slope with respect to P at $(R_s,0)$ whenever criterion A2 is met, while the slope will decrease with increasing P and become negative at high values of P.

If P tends to infinity, the isocline equation ($dR/dt=0$) reduces to:

$$\frac{dR}{dt} = R_{in,max} - c(R)P - r_{min}R = 0$$

which simplifies to:

$$P = \frac{R_{in,max} - r_{min} R}{c(R)}$$

Now P only approaches infinity if $c(R)$ approaches zero, since the numerator is always positive at the resource isocline. In case of the water-limitation model $c(R)$ equals zero at R=0, so the resource isocline approaches R=0 as P approaches infinity. In case of the nutrient-limitation model, $c(R)$ equals zero at $R=R_u$, so the resource isocline approaches $R=R_u$ as P approaches infinity.

Stability analysis

In order to establish the local stability of an equilibrium (R^*,P^*), we investigate the Jacobian matrix of system A1:

$$J = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix} = \begin{pmatrix} -\frac{dc(R^*)}{dR}P^* - r(P^*) & \frac{dR_{in}(P^*)}{dP} - c(R^*) - \frac{dr(P^*)}{dP}R^* \\ \frac{dg(R^*)}{dR}P^* & g(R^*) \end{pmatrix}$$

We consider three equilibria: the boundary equilibrium $(R_s,0)$, and the two internal equilibria (R^*,P_1^*) and (R^*,P_2^*). These equilibria are locally stable if (e.g. Edelstein-Keshet 1988)

(1) $\mathrm{trace}(J) = A_{11} + A_{22} < 0,$

(2) $\det(J) = A_{11}A_{22} - A_{12}A_{21} > 0.$

Boundary equilibrium

At the boundary equilibrium $(R_s,0)$ the stability criteria simplify to $\mathrm{trace}(J)=-r(0)+g(R_s)<0$ and $\det(J)=-r(0)g(R_s)>0$. The determinant is positive as long as $g(R_s)$ is negative, which is a more restrictive criterion for stability than the trace criterion. Hence, the boundary equilibrium is stable whenever $R_s<R^*$, i.e. whenever the resource isocline intersects the P=0 axis to the left of the plant isocline.

Internal equilibria

At the resource-plant equilibria (R^*,P_1^*) and (R^*,P_2^*) the specific growth rate of the plant is (by definition) zero, i.e. $g(R^*)=0$. Hence, the stability criteria simplify to $\mathrm{trace}(J)=-(\mathrm{d}c(R^*)/\mathrm{d}R)P^*-r(P^*)<0$ and $\det(J)=-(\mathrm{d}g(R^*)/\mathrm{d}R)P^*[(\mathrm{d}R_{in}(P^*)/\mathrm{d}P)-c(R^*)-(\mathrm{d}r(P^*)/\mathrm{d}P)R^*]>0$. Since the trace criterion is always satisfied, and $(\mathrm{d}g(R)/\mathrm{d}R)P^*$ is always positive, it follows that any internal equilibrium is stable whenever $(\mathrm{d}R_{in}(P)/\mathrm{d}P)-c(R^*)-(\mathrm{d}r(P)/\mathrm{d}P)R^*<0$. This criterion is met whenever the resource isocline has a negative slope (see above). The slope of the resource isocline is negative at (R^*,P_1^*), while it is positive at (R^*,P_2^*). As a result, the equilibrium at (R^*,P_1^*) is stable, while the equilibrium at (R^*,P_2^*) is an unstable saddle point (see, e.g., Edelstein-Keshet 1988).

Chapter 4

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

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Abstract

There is an urgent need to develop a mechanistic understanding of how site-specific properties can lead to irreversable 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.

Introduction

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 inbuilt 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, Chapter 2 in this thesis). 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 temporal and spatial 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, Chapter 3 in this thesis), 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 irreversable 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:

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

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

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

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

and

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

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

$$W_{in}(P) = PPT\frac{P + k_2W_0}{P + k_2} \tag{5}$$

(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 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:

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

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

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:

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

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

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

The parameter c_{max} follows the water-limitation model. Note that the factor d^*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

$$r_N(P) = r_{N,\max}\frac{k_2}{k_2 + P} \tag{10}$$

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.

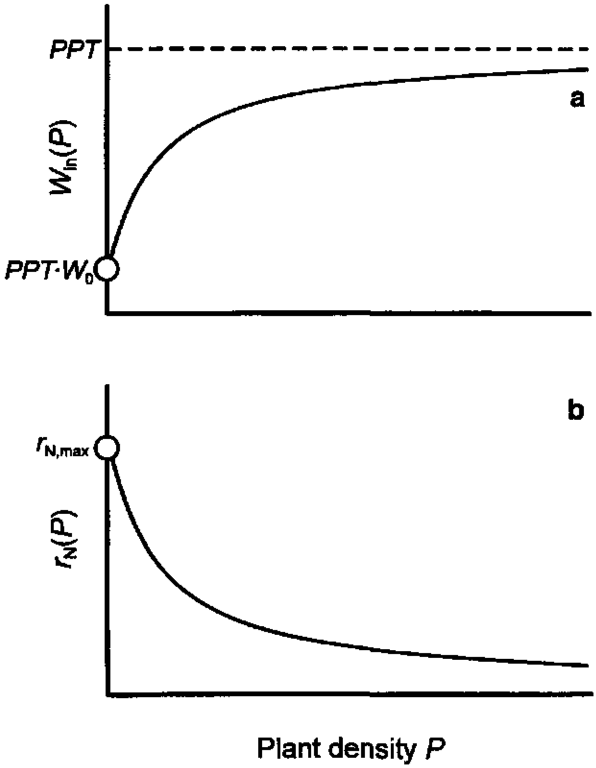


Fig. 1. (a) The shape of the feedback relation between water infiltration W_{in} and plant density P. Parameter values: PPT=2, k_2=5, W_0=0.2. (b) The shape of the feedback relation between the specific nutrient loss r_N and plant density P. Parameter values: $r_{N,max}$=0.5, k_2=25. Symbols as in Table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

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}

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, Chapter 3 in this thesis). 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 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 occuring in the phase plane are seperated 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: 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

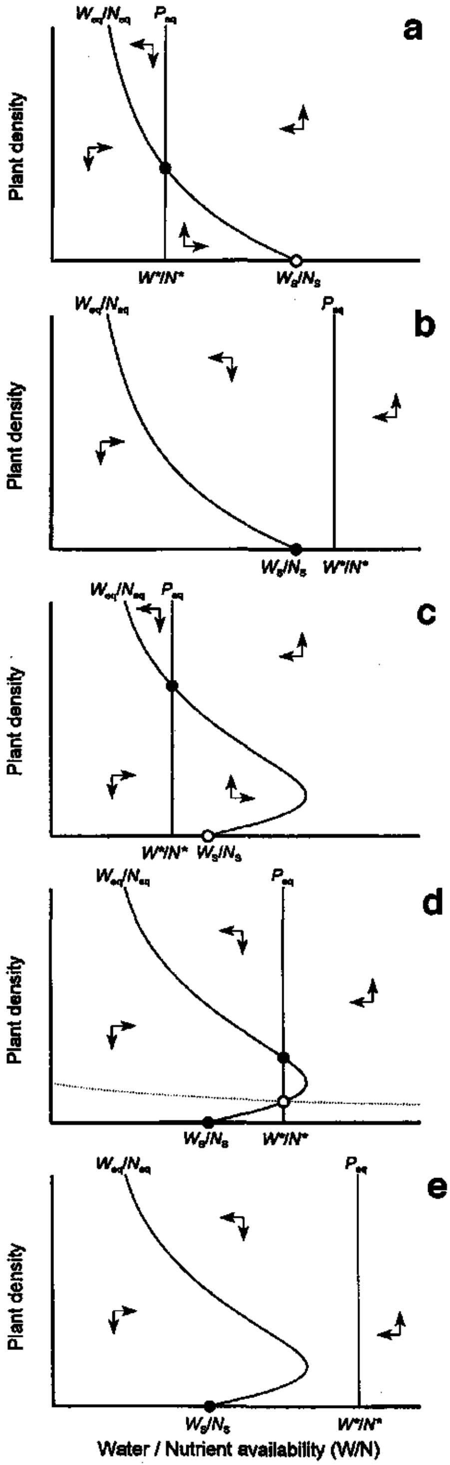


Fig. 2. Phase planes representing five functional states. Phase planes with W on the horizontal axis represent water-limited systems. Phase planes with N on the horizontal axis represent nutrient-limited systems. The combined resource isocline is indicated by W_{eq}/N_{eq} and the combined plant isocline 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.

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 is 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 affect 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.

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 $g_{max}(W/(W+k_1))$ (equation 3). In bare soil, water levels equilibrate at $W=W_s=PPT(W_0/r_W)$ (equation 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 $W^*=W_s$ (equation A1, Appendix), as illustrated in Fig. 2.

Likewise, in case of the nutrient-limitation model, growth equals $g_{max}(N/(N+k_1))$ (equation 8). If plants are absent, then $N=N_s=N_{in}/r_{N,max}$ (equation 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 $N^*=N_s$ (equation 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 by 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 between 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.

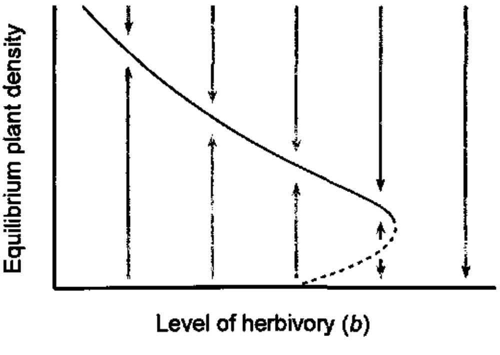


Fig. 3. An example of a catastrophe fold showing the relation between equilibrium plant density P_{eq} and the level of herbivory b. Sudden jumps of plant equilibria occur at distinct levels of herbivory, when the latter follow either an increasing or decreasing path. This property is referred to as 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.

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 out the five functional states (Fig. 2) on the horizontal parameter planes in a graphical way. The 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-limition 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

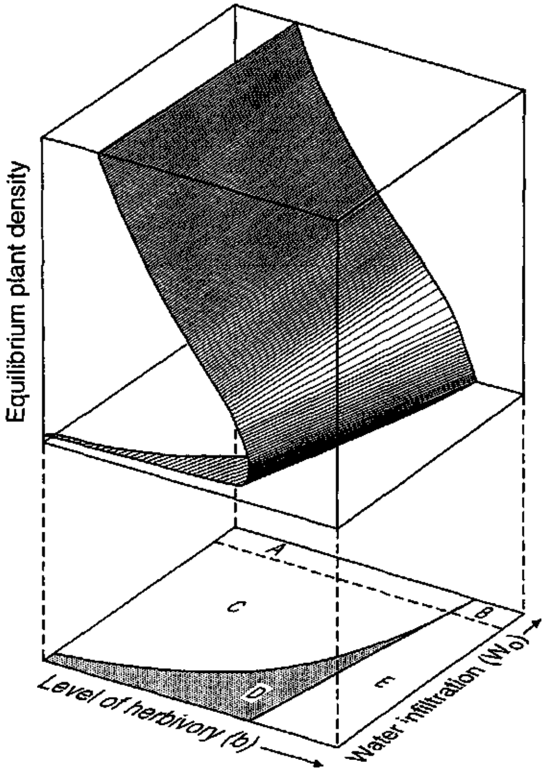
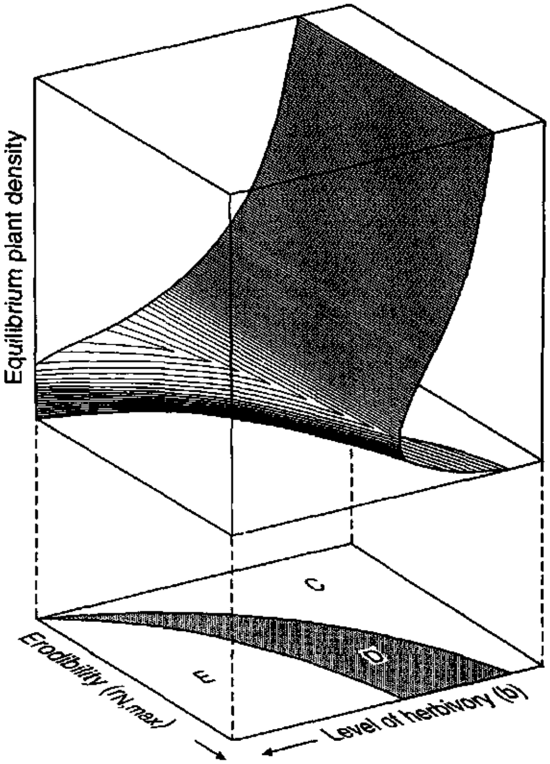


Fig. 4. An example of an equilibrium manifold *showing the equilibrium plant density* P_{eq} as a function of the level of herbivory b and water infiltration W_0. Parameter values: g_{max}=0.5, k_1=3, d=0.1, PPT=2, k_2=5, c_{max}=0.05, r_W=0.1. Symbols as in Table 1. The bifurcation set, outlined by 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)



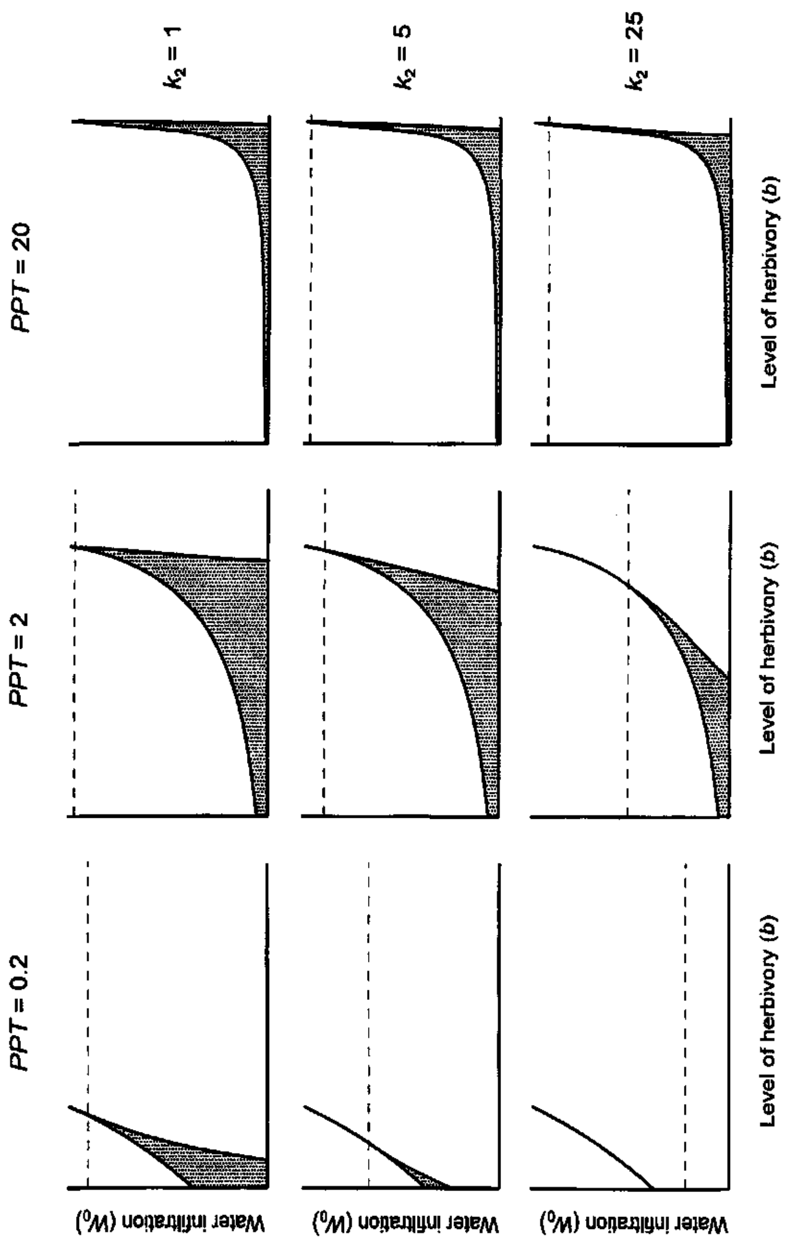


Fig. 6. Bifurcation sets in the parameter planes showing the effect of parameter variations on the qualitative dynamical behaviour of the model systems. The horizontal dashed lines indicate for which parameter combinations a trajectory through the parameter plane will move through the bifurcation set 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.

ranges of herbivory. When the soil is sandy (high W_0), 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 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 herbivores 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-limition 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 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

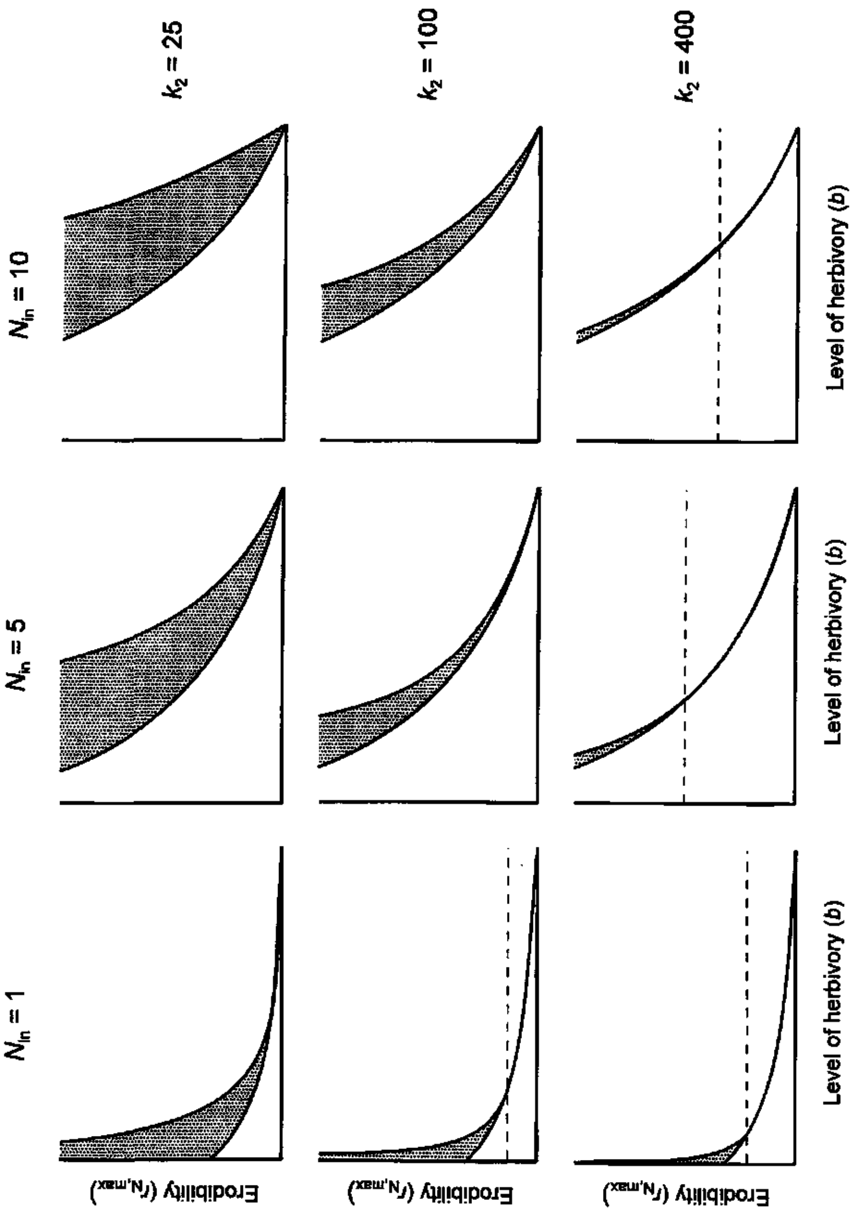


Fig. 7. The functional states are mapped out on the $r_{N,max}$-b parameter plane for different values of N_{in} and k_2. Symbols as in Table 1. Parameter values: g_{max}=0.5, k_1=3, d=0.1, c_{max}=0.05.

as the nutrient retention capacity of vegetation communities (cf. Kellman & 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 irreversable 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 Sudanian 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-clay 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 Sudanian 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 p. 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 run-off 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-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, Chapter 2 in this thesis, Rietkerk and Van de Koppel 1997, Chapter 3 in this thesis).

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 Houerou 1989, Rietkerk et al. 1996, Chapter 2 in this thesis) 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, Chapter 2 in this thesis). 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 p. 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 isocline for the water-limitation model are respectively:

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

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

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 isocline for the nutrient-limitation model are respectively:

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

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

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

$$W_s = PPT \frac{W_0}{r_W} \qquad \text{A3}$$

and

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

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 equation 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

$$\frac{dW_{eq}}{dP}\Big|_{P=0} > 0$$

from which can be derived that

$$\frac{dW_{in}(P)}{dP}\Bigg|_{P=0} > c_{\max} \frac{W}{W + k_1} \qquad \text{A5}$$

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

$$\frac{dN_{eq}}{dP}\Big|_{P=0} > 0$$

from which can be derived that

$$-\frac{dr_N(P)}{dP} N\Bigg|_{P=0} > c_{\max} \frac{N}{N + k_1} - d\frac{c_{\max}}{g_{\max}} \qquad \text{A6}$$

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, $N=k_1d/(g_{max}-d)$ 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 $N=N^*$. W^* and N^* are independent of P, so the plant isocline is a straight, vertical line at $W=W^*$ or $N=N^*$ (Fig. 2).

Chapter 5

Feedback relations between vegetation biomass and soil water content in a semi-arid savanna

Claudius A. D. M. van de Vijver and Max Rietkerk

Submitted

Abstract

In African savanna systems aboveground biomass removal through herbivory and fire affects vegetation production and nutrient content. We investigated the effect of removal of aboveground biomass on soil water content and subsequent effects on grass tuft production and nutrient content in a factorial experiment in a semi-arid savanna in northern Tanzania. We distinguished between removal of grass tufts and litter. We also investigated the mechanisms which accounted for the variation in soil water content when grass tufts and litter were removed. Removal of grass tufts did not significantly affect soil water content, but it did increase grass leaf N content of the remaining tufts. We attribute this effect to increased availability of soil N per individual grass tuft due to the reduction of the number of grass tufts per unit area. Removal of litter caused a significant decline in soil water content which we ascribe to an increased loss of water through evaporation. This effect outbalanced the reduced interception of rainfall when litter was removed. Removal of litter additionally reduced grass leaf P content. Removal of grass tufts did not affect production of the remaining tufts over the experimental period but removal of litter did. We conclude that this effect primarily was mediated by a reduced soil water content in the absence of litter, rather than a reduced grass leaf P content, since soil P was not a main limiting factor during the experimental period. Fire removes both standing biomass and litter, while herbivores primarily select green standing biomass. We therefore suggest that the effect of aboveground biomass removal through fire on vegetation production and nutrient content, via changes in soil water content, is greater than the effect of aboveground biomass removal through herbivores.

Introduction

It has long been recognised that fire and herbivory affect vegetation production and nutrient content in savanna systems through a variety of direct and indirect effects (Frost and Robertson 1985, McNaughton 1985, Ruess 1985). This especially is the case for African savanna systems where high levels of wildlife and livestock grazing and reoccurring, mainly anthropogenic, fires have affected savanna ecosystems for millennia (Walker 1981).

One of the effects of fire and herbivory on vegetation production and nutrient content operates through the removal of aboveground biomass. This results in changes in the plant's physiology, due to rejuvenation of plant material, and reallocation of carbon and nutrients as result of changes in shoot:root ratios. Furthermore, removed biomass by fire and herbivores is deposited back to the system in the form of ash and dung respectively, hence increasing nutrient availability (McNaughton 1985).

Besides these factors mentioned, biomass removal also affects vegetation production and nutrient content by altering soil water content, which is the main factor determining annual production in semi-arid savanna systems (Walker 1981, Goldstein and Sarmiento 1985). In this study, we focus on the effects of aboveground biomass removal on soil water content and the consequences for production and nutrient content of the vegetation in a semi-arid savanna. Soil water content is determined by the amount of water that infiltrates into the soil (I) and the amount of infiltrated water that is subsequently lost through evapotranspiration (E) and drainage (D). Thus, the change in soil water content in the rooting zone (ΔS) is

$$\Delta S = I - (E + D) \tag{1}$$

where

$$I = P - (E_i + R) \tag{2}$$

and where P is the amount of rainfall, and E_i and R are loss of rain water through interception and run-off respectively. These determinants of soil water content are not only affected by amount and intensity of rain, slope and soil physical properties but also by aboveground biomass (Kelly and Walker 1976, Fischer and Turner 1978, Van Wijngaarden 1985, Dunin 1987). Aboveground biomass can have positive as well as negative effects on soil water content. Positive effects are through reduced run-off, increased infiltration rates and lower evaporation rates, and negative effects are through increased interception and transpiration, due to increased area transpiring surface (Savage 1980, Eldridge 1993). Thus, the net effect of aboveground biomass removal on soil water content depends on the balance between these processes. Furthermore, this effect is influenced by the extent and frequency of biomass removal. In situations of intensive biomass removal over several decades a decline in soil water primarily is attributed to increased levels of run-off (Redmann 1978, Knapp 1984). But if biomass removal is moderate, soil water content may be enhanced due to reduced levels of interception (Cass et al 1984, Dunin 1987). This especially is the case when rain falls in a large amount of small rain showers, since in this situation the amount intercepted, relative to the total amount fallen, increases (Scholes and Walker 1993).

Finally, the effect of biomass removal on the soil water content also depends on whether the removed biomass consists of live or dead material, such as litter. Litter is amorphous, primarily affecting evaporation rates, while standing biomass, which also consists of live, transpiring material in the growing season, also affects the amount of water that is lost through transpiration. Moreover, since litter is compacted to the ground, it tends to have a stronger positive effect on infiltration than standing biomass, while it also reduces soil evaporation due to reduced soil temperature and wind speed at soil surface (Kelly and Walker 1976, Savage 1980).

Although fire and herbivores both remove aboveground biomass, they differ in the selectivity in which this occurs. Fire is non-selective, removing the bulk of biomass and litter whereas herbivores are selective, primarily consuming green, palatable plant material (Prins and Beekman 1989). On the basis of the aforementioned it can be expected that there will be variation in the effects of biomass removal by herbivory or fire on soil water content and subsequently vegetation production and nutrient content.

In this study we investigated how different levels of aboveground biomass removal, as well as composition of biomass removed (i.e. standing biomass or litter) affects soil water content and subsequently vegetation production and nutrient content. To this end, we measured soil water content, production and nutrient content of grass tufts in a semi-arid savanna during a rainy season in untreated plots and plots from which litter and various amounts of standing biomass was removed. Additionally, we investigated the mechanisms through which aboveground biomass affects soil water content (i.e. the effect on the different soil water balance parameters, see Equations 1 and 2) by performing rain simulation experiments in which the water content of soil and vegetation was monitored for several days.

Methods

Study area

The study was carried out on the eastern boundary of Tarangire National Park, situated on the eastern side of the Great Rift Valley in Northern Tanzania (4° S, 37° E). The topography is gently undulating with slopes between 1 and 3%. Soils are deep to very deep, well drained, red sandy loams of Precambrian origin. Mean annual rainfall is 452 mm but is very variable within and between seasons. The rainy season extends from December to May with a peak in March and April. Average maximum temperature is 27°C and average minimum is 16°C. The vegetation is a wooded savanna with a tree cover of approximately 5%, primarily consisting of

Commiphora-, *Combretum-* and *Acacia* species. Grass cover is well developed and is dominated by tufted perennial grasses. Dominant grasses are *Themeda triandra*, *Heteropogon contortus* and *Sehima nervosa*. Herb cover in the research area is negligible.

The vegetation is prone to regular burning due to high production of grass biomass and high occurrence of fires; on average the area burns once every three years (Van de Vijver, unpubl.). Herbivory occurs by large migratory herds of ungulates (common wildebeest and Burchels zebra) which pass through at the beginning and end of the wet season and by residential African buffalo, African elephant and impala (Kahurananga and Silkiluwasha 1997).

Rainfall data

A self-registering rain gauge with data logger (Eijkelkamp Agrisearch Equipment b.v., The Netherlands) was used to measure the amount, distribution and intensity of rain showers over the season. Data were collected from August 1993 to August 1996. Recording interval of the logger was 30 minutes. A rainfall event was recorded as one separate shower when the time interval between rainfall events was more than 1 hour. Yearly rainfall averages were obtained by summing the amounts of individual showers between August and July (after Prins and Loth, 1988).

Experimental design

The research consisted of three separate experiments. The first experiment was set up to investigate the effect of biomass removal on soil water content and consequently grass production and nutrient content (*Experiment 1*). The second was a rain simulation experiment to investigate which parameters of the soil water balance (Equations 1 and 2) cause the changes in soil water content due to biomass removal. (*Experiment 2*). The third experiment was performed to investigate how the amount of rain water intercepted is affected by biomass (live and dead) and rainfall amount (*Experiment 3*), since we expected interception to have an important effect on soil water content (Cass et al 1984, Scholes and Walker 1993).

Experiment 1

We selected a total of 30 experimental plots of 5 x 5 m via stratified random sampling in an area of one hectare whereby trees, shrubs and termite mounds were avoided. We imposed treatments by manually removing predetermined amounts of biomass whereby we distinguished between removal of whole grass tufts (tuft treatment) and removal of litter (litter treatment). Tuft treatment consisted of three levels: '75' which was the field situation (control) of approximately 75% tuft cover, '50' in which tuft cover was reduced to 50% and '25' in which tuft cover was reduced to 25%. We reduced tuft cover by cutting away randomly selected grass tufts below the apical meristem, to prevent resprouting during the experiment. Removal of tufts led to the following tuft density: 3.2 tufts per m^2 for the '75' tuft treatment, 2.0 for the '50' tuft treatment and 1.6 for the '25' tuft treatment. Litter treatment consisted of two levels: total removal of litter (-) and no removal (+). Thus there were six treatments (75+, 75-, 50+, 50-, 25+ and 25-), each being replicated five times. The experimental trial ran from March to August 1996.

To determine soil water content we collected soil samples five times during the research period (March, April, May, June and July) with a metal pipe (Ø = 4.2 cm) at four different soil depths (0-10, 10-20 20-30 and 30-40 cm). Per plot and depth we took two sub-samples which we bulked to reduce variability. Soil water content was measured gravimetrically.

To determine the effect of aboveground biomass removal on grass water content, which may change due to alterations in soil water content and changes in microclimatic conditions (Savage 1980), we measured the grass water content in the different treatments on the same dates that the soil samples were taken. We used the relative water content of young, fully expanded grass leaves as a measure of variation in grass water content in the different treatments (Schmidt and Kaiser 1987, Lo Gullo and Salleo 1988). Samples were taken at 09.00 am, 01.00 pm and 05.00 pm (East African Standard Time). Approximately five grams of fully expanded young grass leaves were collected per plot and weighed (W_{field}). Samples were then placed in water for 24 hours and weighed again after removal of hanging water (W_{H2O}). Finally, samples were dried (60 °C, 48 hours) to obtain dry weight (W_{dry}). Relative grass leaf water content was subsequently calculated as: $(W_{field} - W_{dry}) / (W_{H2O} - W_{dry})$. Grass leaf samples used for determining relative water content were also used to analyse nitrogen (N) and phosphorus (P) content of grass leaf material. Hereby, we bulked the samples that were taken at three different times in the day. Prior to chemical analysis samples were ground through a 1 mm sieve and digested using a modified Kjeldahl procedure with Se as a catalyst (Chapman 1976). N and P content was measured colorimetrically with a continuous flow analyser (Skalar SA-4000).

We estimated production by comparing air dried biomass of grass tufts at the beginning of the research period (March) with the biomass at the end (August), whereby a correction was made for decomposition (Cox and Waithaka 1989). We used five randomly selected tufts that were removed for the '50' and '25' tuft treatments at the beginning of the experiment to estimate average tuft biomass in March. At the end of the experiment we harvested all tufts and litter from the plots and here five randomly selected tufts were used to estimate average tuft biomass per treatment in August. Difference in biomass allocation between treatments was measured by weighing sorted leaf, stem and dead biomass.

We analysed treatment effects on soil water content and grass production, nutrient and water content using a full factorial ANOVA. If necessary data were transformed to meet with the conditions for ANOVA (log transformation for biomass data and arcsine for ratios) (Sokal and Rolff 1981). Differences between means were analysed with a Tukey-HSD test.

Experiment 2

We investigated the effect of biomass removal on the various parameters affecting soil water content by measuring the soil and grass water content for three days, after 7 mm of rain was applied over a period of 10 minutes to 2 x 1 m plots which varied in tuft cover and presence of litter. The 7 mm rain shower was used since this represents a typical rain shower (based on 4 years of rainfall data collected at Park Head Quarters situated 40 km north-west of the research area). Tuft and litter treatments were obtained in the same manner as in the previous experiment, but the 50+ and 50- treatments were left out. Thus, there were four treatments (75+, 75-, 25+ and 25-). Each treatment was replicated five times and the experiment was carried out twice, once in the wet season (April 1996) and once in the post-rain period (July 1996). We simulated rain showers with a watering can with a one metre wide nozzle which distributed water over the plots evenly.

We measured soil water content in the same way as in the previous experiment, but the 30-40 cm soil depth was not sampled. Variation in infiltration was estimated by comparing the soil water content in the different treatments 30 minutes after applying 7 mm of rain (T1). We estimated water loss through evapotranspiration and percolation to deeper layers of the rooting zone by comparing T1 with the soil water content 1 day after (T2) and two days after (T3) rain simulation. Treatment effects on relative grass water content were analysed by comparing the relative water content of young, fully expanded grass leaves on the T2 and T3 soil sampling dates at 09.00 am, 01.00 pm and 05.00 pm. Procedures were the same as in *Experiment 1*. Since the majority of grass water data collected during the wet season trial (April 1996) were lost, analysis of grass water data was restricted to the post-rain period trial (July 1996). Data analysis occurred as explained for the previous experiment.

Experiment 3

Firstly, we investigated the effect of amount of rainfall and aboveground biomass (including and excluding litter) on the amount of rain intercepted by simulating three different rain showers (7, 3 and 1.5 mm respectively) over a period of 10 minutes on 2 x 1 m plots which varied in tuft biomass and presence or absence of litter. Within 30 minutes after rain simulation, all biomass from the plots was harvested and weighed, whereafter it was dried and weighed again. After subtraction of the vegetation water content, which we obtained from unrained control plots, we compared the amount of water that was intercepted for the different treatments. Replication per treatment was five.

Secondly, we investigated the effect of the weight percentage of dead grass material on interception by applying 7 mm of rain over a period of 10 minutes on 2 x 1 m plots for which the percentage of dead grass material was estimated. Plots were categorized in four different groups: 100%, 75%, 50% and 25% dead grass material, using four replicates.

Finally, we measured the total amount of water that potentially could be intercepted by the vegetation by harvesting all biomass from 1 x 1 m plots, weighing it, soaking it with water in a drum and weighing it again. Here, we compared two treatments: with and without litter, using five replicates.

Since biomass was a continuous variable in the first mentioned interception experiment, we analysed the data with an ANCOVA with litter and rain as main effects and biomass as co-variate. The effect of weight percentage of dead grass material on interception was analysed with a one-way ANOVA. Finally, the total amount of water that was intercepted by biomass, expressed in gram water per gram biomass, was compared with that of the 1.5, 3 and 7 mm of rain in an ANOVA with rain and litter as main factors.

Results

Rainfall data

Total rainfall in the 1995-1996 season was 513 mm. The highest proportion of total rainfall within this season fell in February, March and April (30, 20 and 30 % of total respectively). Total rainfall in the 1995-1996 season was higher than the mean annual rainfall over the three seasons in the 1993-1996 period (452 mm), which was produced by an average of 70 rain showers per season. Rain showers up to 10 mm accounted for approximately 80% of the rain events (Fig. 1). These showers, however, only contributed about 30 % to the mean annual rainfall, while intensive rain showers of more than 65 mm are rare but produce about 25 % of the mean annual rainfall.

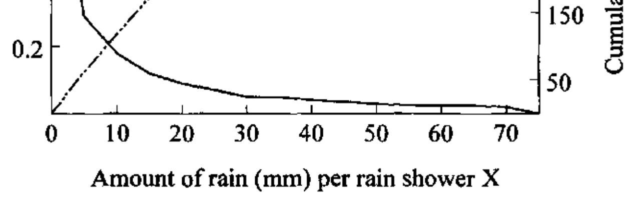

Fig. 1. The cumulative amount of annual rainfall produced by rain showers of X mm (= — - - —) and the probability distribution of a rain shower exceeding X mm (P(x>X) = —). Three year daily rainfall records were used for rainfall averages and to calculate the probability distribution (August 1993 - July 1996). Average total number of showers per year is 70, average annual rainfall = 452 mm.

Experiment 1

Soil water content

Tuft treatment did not significantly affect soil water content while removal of litter significantly reduced soil water content (Table 1, Fig. 2). Analysis of variance, with soil depth included as factor (Table 1), revealed that the effect of litter was affected by soil depth whereby the effect primarily was restricted to the 0-10 cm soil layer. The effect of litter, however, depended on sampling date which was due to a reduced effect of litter on the soil water content as soil water content declined after the rains had stopped and soils started to dry up.

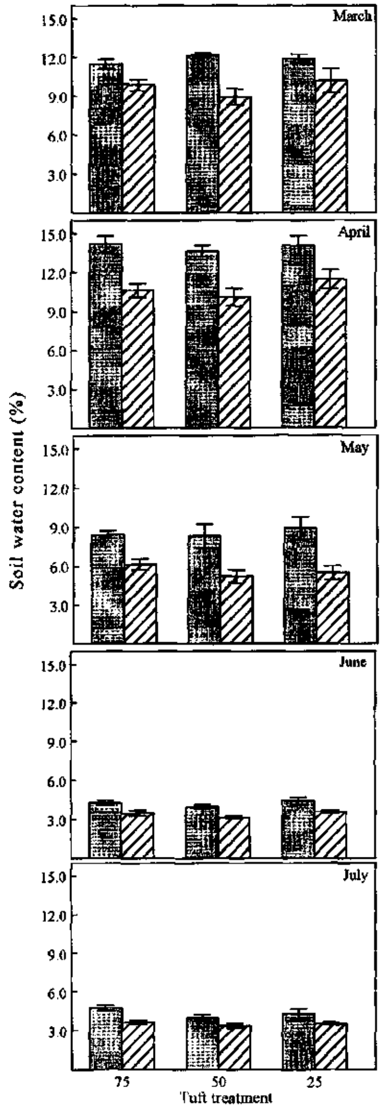

Fig. 2. Soil water content (weight %, ± SE, n = 5) of the 0-10 cm soil depth in plots varying in tuft cover ('75', '50' and '25'), with litter (dark bars) and without litter (hatched bars) on five different dates in the growing season.

Table 1. F-values and levels of significance (*:$p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ns = not significant, n = 5) as a result of ANOVA with soil water content, grass leaf water, N and P content, N:P ratios, production of grass tufts and leaf weight ratios (LWR) as dependent variables, and litter (L), tuft cover (T), date of sampling (S), depth of sampling (D) and hour of sampling (H) as factors. - indicates that the factor or interaction concerned was not in the design. If not significant, higher order interactions are not shown.

	Soil water content (%)	Soil water content total profile (%)	Relative grass leaf water content (%)	Grass leaf N (%)	Grass leaf P (%)	Grass leaf N:P ratio	Grass tuft production (g day $^{-1}$)	LWR
L	123.58***	58.03***	7.84**	3.09^{ns}	4.03*	12.79**	19.44***	1.15^{ns}
T	2.59^{ns}	0.60^{ns}	5.01**	27.85***	0.09^{ns}	8.73***	0.51^{ns}	8.01**
S	1083.85***	563.19***	99.68***	119.75***	33.03***	10.81***	-	-
D	279.36***	-	-	-	-	-	-	-
H	-	-	25.43***	-	-	-	-	-
LxT	1.46^{ns}	1.25^{ns}	3.1*	0.12^{ns}	0.67^{ns}	2.31^{ns}	2.14^{ns}	0.49^{ns}
LxS	5.18***	2.52*	1.39^{ns}	1.36^{ns}	1.44^{ns}	1.11^{ns}	-	-
LxD	20.76***	-	-	-	-	-	-	-
LxH	-	-	0.11^{ns}	-	-	-	-	-
TxS	2.33*	1.58^{ns}	3.61***	0.23^{ns}	1.27^{ns}	1.80^{ns}	-	-
TxD	1.65^{ns}	-	-	-	-	-	-	-
TxH	-	-	0.58^{ns}	-	-	-	-	-
SxD	76.44***	-	-	-	-	-	-	-
SxH	-	-	5.21***	-	-	-	-	-
LxSxD	2.75**	-	-	-	-	-	-	-

Grass leaf water content

Both removal of litter and grass tufts affected grass water content significantly (Table 1, Fig. 3). Litter removal generally led to a reduction in grass leaf water content, while removal of grass tufts generally led to an increase in grass water content. These effects, however, were only apparent in the post-rain period (July, August) whereby the reduction of grass water content due to the reduction of litter primarily was restricted to the '25' tuft treatment (Fig. 3)

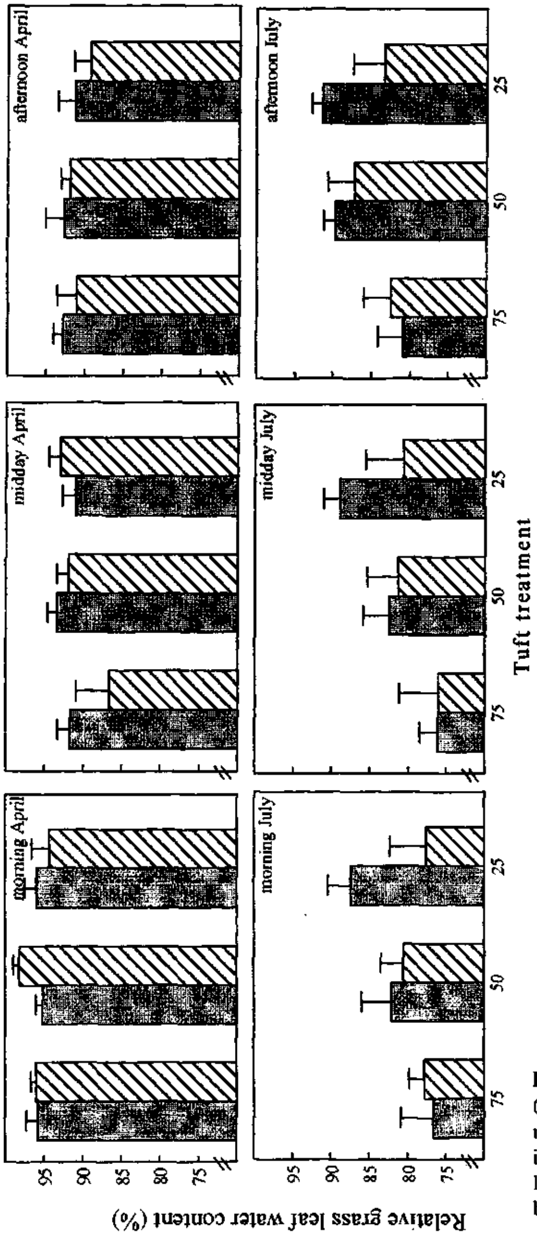

Fig. 3. Relative grass leaf water content (weight %, ± SE, n = 5) measured in the morning, noon and afternoon in plots varying in tuft cover ('75', '50' and '25'), with litter (dark bars) and without litter (hatched bars), in April and July.

Grass tuft production

Individual grass tuft production (g day^{-1}) in plots with litter was higher than those without litter (Table 1, Fig. 4a). Fig. 4a suggests that response of grass tuft production to litter was dependant on tuft cover, but this interaction was not significant. Although tuft cover did not affect production it did affect the live leaf weight ratio (LWR, live leaf weight per total tuft weight), the LWR increasing with decreasing tuft cover (Table 1, Fig. 4b).

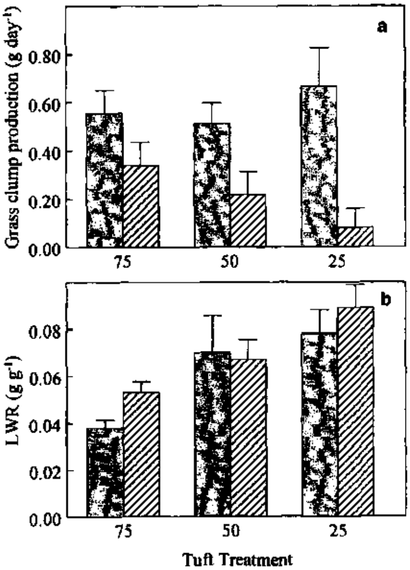

Fig. 4. (a) Grass tuft production and (b) ratio of leaf weight to total weight (LWR) (± SE, n = 5) in plots varying in tuft cover ('75', '50' and '25') with litter (dark bars) and without litter (hatched bars).

N and P content

The N and P content of young grass leaves decreased significantly during the season (Table 1, Fig. 5). The P content of young grass leaves in plots with litter was higher than in plots without. Plots with litter tended to have a lower grass leaf N content than plots without litter, but this effect was not significant. N content increased significantly with decreasing tuft cover, while P content did not vary significantly with tuft cover.

To determine if N or P was most limiting for growth, we analysed N:P ratios of grass leaves during the season for different tuft and litter treatments (Verhoeven et al. 1996, Koerselman and Meuleman 1996). N is most limiting if N:P ratios are below 6.67, whereas P is most limiting if the ratios are above 25 (Penning de Vries and Djitèye 1991). During our experiments, N was more limiting than P, since N:P ratios fluctuated around 6.67 for all data and treatments sampled.

ANOVA also revealed that litter significantly reduced the N:P ratio, which was a result of increased P content in grass leaves in treatments with litter, while the ratios significantly decreased with increasing tuft cover due a decline in N content (Table 1, Fig. 5).

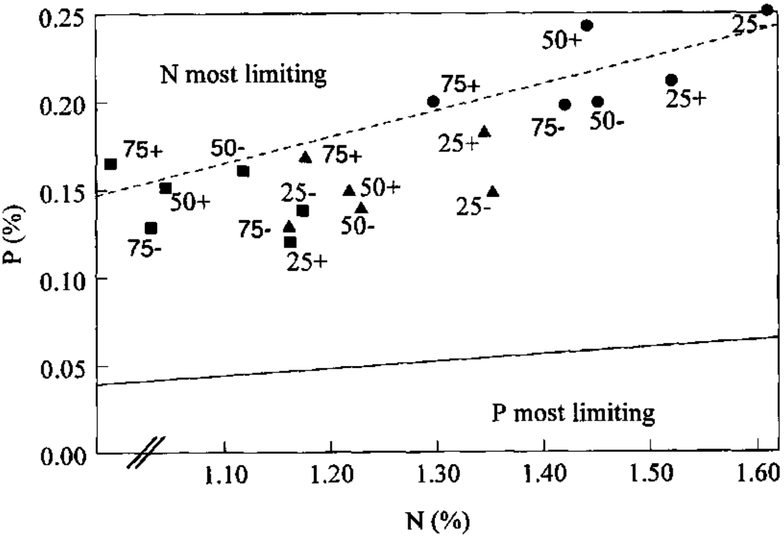

Fig. 5. Grass leaf N and P content (%) in plots varying in tuft cover ('75', '50' and '25' resp.) and litter (+ = with litter, - = without litter) in April (●), June (▲) and July (■).
——— : N:P ratio = 25,------- : N:P ratio = 6.7.

Experiment 2

Soil water content

Significant time and litter effects were were primarily restricted to the 0-10 cm soil layer. At T1, plots with litter had a dryer 0-10 cm soil layer than plots without litter, while at T2 and T3 the reverse was true (Table 2, Fig. 6). No significant effect of tuft removal on soil water content was found.

Grass leaf water content

A significant decline was found in relative grass water content between the day after rain simulation and the following day (T2 and T3 respectively) (Table 2, Fig. 7) The decline, however, depended on tuft treatment since the '75' tuft treatment showed no significant decline while the '25' tuft treatment did ($p \leq 0.01$). No significant effects were found for litter.

Table 2. F-values and levels of significance (*:$p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ns = not significant, n = 5) as a result of ANOVA with soil water content and relative grass leaf water content after 7 mm rain simulations as dependent variables, and litter (L), tuft cover (T), interval after rain simulations (I), depth of sampling (D) and hour of sampling (H) as factors. - indicates that the factor or interaction concerned was not in the design. If not significant, higher order interactions are not shown.

	Soil water content (April) (%)	Soil water content (July) (%)	Relative grass leaf water content (July) (%)
L	13.1***	0.28^{ns}	1.57^{ns}
T	0.21^{ns}	2.51^{ns}	1.41^{ns}
I	10.52***	2.88^{ns}	19.27***
D	38.84***	43.52***	-
H	-	-	0.67^{ns}
LxT	0.29^{ns}	0.40^{ns}	0.94^{ns}
LxI	6.08**	2.33^{ns}	1.18^{ns}
LxD	2.69*	3.12*	-
LxH	-	-	0.36^{ns}
TxI	0.78^{ns}	0.151^{ns}	8.74**
TxD	2.81^{ns}	1.19^{ns}	-
TxH	-	-	0.13^{ns}
IxD	8.33***	5.39***	-
IxH	-	-	1.74^{ns}
LxIxD	3.09*	2.49*	-

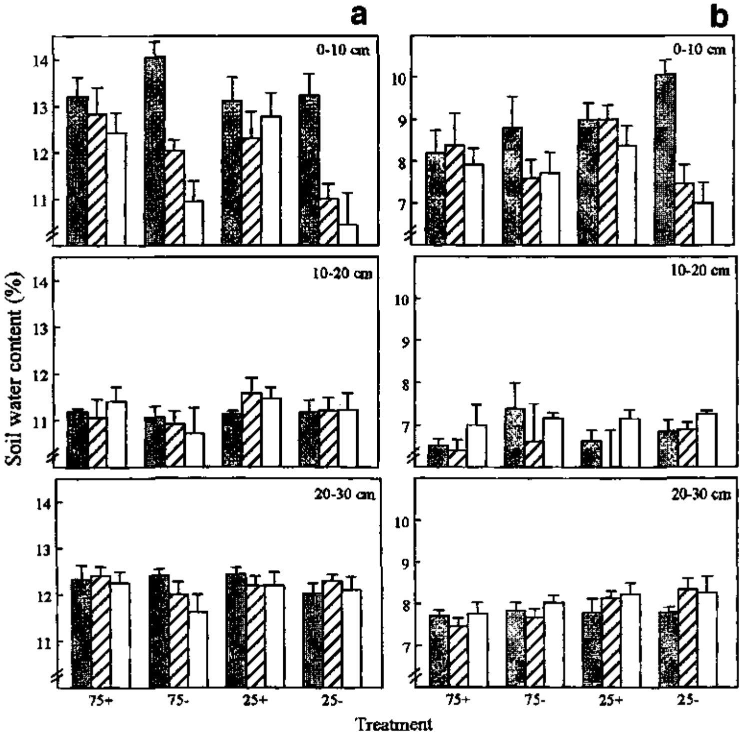

Fig. 6. Soil water content (weight %, ±SE, n = 5) in different soil layers (0-10, 10-20 , 20-30 cm) in plots varying in tuft cover (75 and 25 %) and litter (+ = with litter, - = without litter) half an hour after (T1, dark bars), 1 day after (T2, hatched bars) and 2 days after (T3, open bars) administering 7 mm of water in (a) April and (b) July.

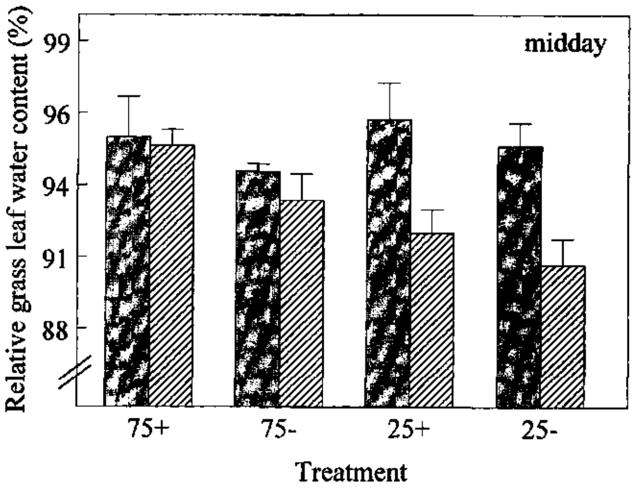

Fig. 7. Relative grass leaf water content (%, ± SE, n = 5) of young grass leaves at midday in plots varying in tuft cover (75 and 25 %) and litter (+ = with litter, - = without litter) 1 day after (T2, dark bars) and 2 days after (T3, hatched bars) administering 7 mm of water in the July rain simulation experiment.

Experiment 3

Since we observed no run-off during rain simulation, variance in the amount of water infiltrating into the soil could be attributed to interception (see Equation 2). The amount of water intercepted (g_{water} m^{-2}) significantly increased with aboveground biomass (Table 3). After removal of the biomass effect, we found a significantly higher interception in plots with litter than in plots without litter and interception significantly increased with rainfall. Similar results were found when interception was expressed in mm of rain intercepted (Tables 3, 4). Expressed as a percentage of the amount of rain applied, interception significantly declined with increasing rainfall. Hereby, an interaction with litter was found. This was caused by a significant higher percentage intercepted in the plots with litter than in the plots without litter for the 1.5 and 3 mm rain treatments, while litter did not significantly affect the percentage intercepted in the 7 mm rain treatment. The percentage of rain water intercepted reached up to 58% in plots with litter if rain showers of 1.5 mm were applied (Tables 3, 4).

The maximum amount of water intercepted by grass vegetation was 1.74 g_{water} $g_{biomass}^{-1}$ and 1.48 g_{water} $g_{biomass}^{-1}$ for litter and non-litter plots, respectively. These values were not significantly different from the interception during the experimentally applied 7 mm rain shower which were 1.59 g_{water} $g_{biomass}^{-1}$ and 1.44 g_{water} $g_{biomass}^{-1}$ for litter and non-litter plots, respectively. Finally, grass tufts with a high proportion of dead material intercepted significantly more rainfall than tufts with a low proportion of dead material (Fig. 8).

Table 3. F-values and levels of significance (*:$p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ns = not significant, n = 5) as a result of ANCOVA with interception of rainwater by aboveground herbaceous biomass as dependant variable, litter and rain amount applied as factors, and biomass as co-variate. Interception is expressed in: gram water m^{-2}, mm and percentage of rainfall intercepted.

Dependent Interception	Litter	**Factor** Rain (mm)	Litter x Rain	**Co-variate** Biomass
g_{water} m^{-2}	8.83**	4.97**	0.67^{ns}	6.00*
mm	20.26***	3.93*	0.33^{ns}	38.68***
%	15.08**	55.86***	16.40***	26.51***

Table 4. Interception by aboveground biomass (expressed in mm of rainfall intercepted and % of the amount of rainfall applied) in plots with litter (+) and without litter (-) and for different amounts of rainfall applied. Average biomass of plots with and without litter was 698 and 479 g m^{-2} respectively.

	Rain (mm)					
	1.5 **Litter**		**3** **Litter**		**7** **Litter**	
Interception	+	-	+	-	+	-
mm	0.87	0.50	0.99	0.50	1.11	0.69
%	58	33	33	17	16	10

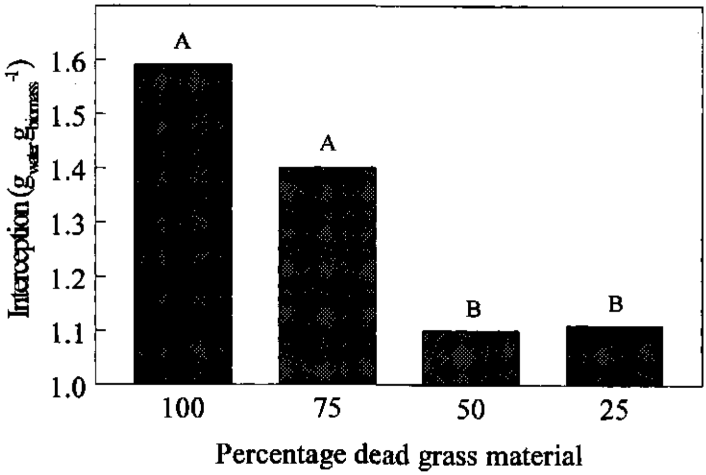

Fig. 8. Amount of water intercepted (g_{water} $g_{biomass}^{-1}$) for biomass varying in the weight percentage of dead material. Capital letters denote significant differences between means for $p \leq 0.05$.

Discussion

Herbivory and fire affect vegetation production and nutrient content by removing aboveground biomass (Frost and Robertson 1985, McNaughton 1985, Ruess 1985). We investigated how aboveground biomass removal affects soil water content and the consequences of this effect on grass tuft production and nutrient content. Tuft removal did not affect soil water content over the season while removal of litter clearly reduced the soil water content over the season (Table 1, Fig. 2). This effect, however, declined as soils became drier in the post-rain period (June, July) and also primarily was restricted to the 0-10 cm soil layer. This arises the question which parameters that affect soil water content (Equations 1 and 2) caused these effects.

At the onset of rain, the first effect that aboveground biomass has on the soil water balance is through interception of rain water which evaporates from the vegetation without even reaching the soil (Daubenmire 1968, Scholes and Walker 1993). We found that interception, expressed in g_{water} m^{-2} and mm, increased with increasing biomass, rainfall and the presence of litter (Tables 3, 4). Higher interception for biomass with litter can be ascribed to the lack of a wax layer and broken cell wall structure in dead plant material which accordingly allows a higher absorption of water. The maximum amount of water that grass vegetation can intercept (g_{water} $g_{biomass}^{-1}$) did not differ from the interception during a 7 mm rain shower. This suggests that above 7 mm of rainfall no additional rainfall is intercepted by the vegetation. Hence, with an annual rainfall of 452 mm, distributed over 70 showers, and an average grass biomass including litter of 698 g m^2 annual interception in the research area would probably range somewhere between 61 mm and 78 mm, which is 13 to 17 % of annual rainfall. This is in line with Dunin (1987) and Scholes and Walker (1993), who found values of 11 and 18.5 % respectively. As heavy showers are infrequent, the light showers are of greater importance for keeping up the soil water content during the growing season (Fischer and Turner 1978). Since it is especially during these light showers that interception is relatively high (Table 4), our data therefore suggest that, especially when vegetation contains much dead material, total annual interception can have a significant effect on the soil water content over the growing season and hence affect vegetation production.

However, removal of litter reduced the soil water content during the experimental period (Fig. 2). This indicates that positive effects of litter on soil water content somehow outbalanced the negative effect of litter through interception. Litter can have a positive effect on soil water content by reducing run-off and loss of infiltrated water through evaporation (Kelly and Walker 1974, Fischer and Turner 1978, Cass et al. 1983). The 7 mm of rain applied in a period of 10 minutes in the rain simulation of *Experiment 2* did not cause run-off. Soil water content even tended to be higher in plots without litter immediately after rain simulation (T1) (Fig. 6) which can only be explained by lower levels of interception. The reason that we found no run-off can be ascribed to the high infiltration rate of the soil in the research area, which was a sandy loam, and that rain primarily occurred in light showers of several millimetres. Furthermore, as biomass removal only occurred at the start of the experiment, changes in soil physical properties which reduce infiltration rates had not yet taken place. Present data therefore suggest that under these conditions run-off is a less prominent factor in the soil water balance and will therefore be less affected by removal of aboveground biomass (see also Snyman and Fouché 1991, Veenendaal 1991, Eldridge 1993, Scholes and Walker 1993). Consequently, the positive effect of litter on the soil water content must be ascribed to reduced loss of infiltrated water (Equations 1 and 2). This is supported by data from the rain simulation experiment (*Experiment 2*) as decline in soil water content in the days after rain simulation was significant in plots where litter was removed while no significant decline was found in plots with litter.

Loss of infiltrated water can be the result of evapotranspiration and percolation of water into deeper layers. Data from the rain simulation experiment also show that loss through percolation cannot explain the decline of soil water in the 0-10 cm soil layer, since this did not result in an increase in the deeper soil layers (Figs 6a, b). This finding is in line with Fischer and Turner (1978), Scholes and Walker (1993) and Snyman (1993), who found that percolation of water into deeper soil layers only plays an important role during exceptionally wet years. Therefore, loss of soil water must be attributed to evapotranspiration.

The rain simulation of *Experiment 2* showed that the tuft treatment did not significantly affect loss of soil water, while the effect of litter primarily was restricted to the 0-10 cm soil layer (Fig. 6). Since litter is amorphous, primarily affecting evaporation and since loss of soil water through evaporation only occurs from the top soil, data suggest that variation in loss due to litter removal primarily is attributed to changes in evaporation rates. This effect is due to the insulatory effect of litter which decreases convective vapour loss to the air and keeps soil temperature lower than bare soil (Kelly and Walker 1976, Chase and Boudouresque 1987). For example, midday temperatures of top soil where litter is removed can be 12 ° C higher than top soil where litter is present (pers. obs., Savage 1980). However, after the rains stopped and the soil started drying up, the positive insulatory effect of litter declined.

Thus, we conclude that the higher soil water content in plots with litter during the season (Fig. 2) is the result of reduced evaporation, whereby this positive effect on soil water content more than compensated for the negative effect of interception.

Removal of litter led to decline in soil water content and grass tuft production during the growing season while removal of tufts did not. This reduced production does not only have to be the result of a decline in soil water content, but could also be due to reduced soil nutrients which are the second limiting factor for plant growth in semi-arid savanna systems, N and P in particular (Walker 1981, Medina 1987). Hereby, besides their individual content, the ratio of these nutrients in plant material is of importance in determining which of the two is most limiting for growth (Verhoeven et al. 1996). Removal of litter caused a decline in grass leaf P content but did not significantly affect grass leaf N content. Hence, reduced grass tuft production in plots without litter may also be the result of reduced P content. However, since N:P ratios indicate that P was not a main limiting factor (Medina 1987, Penning de Vries and Djitèye 1991, Lüttge 1997), and grass leaf N content was not affected by litter removal, we ascribe the observed decline in production after litter removal to a decline in soil water content, and not to a decline in grass leaf P content.

Fig. 4a suggests that the negative effect of litter removal on production increased with decreasing tuft cover, an effect that was not observed for the soil water content. Besides affecting the soil water balance, removal of aboveground biomass also affects microclimatic conditions by increasing surface wind speed, air temperature, radiant flux density and by reducing relative air humidity, which accordingly affect vegetation water content (Knapp 1984, Savage 1980). This can result in reduced relative grass water content when transpired water is not replenished, and can thus explain the lower relative grass water content in the '25' tuft plots without litter at the end of the rainy season in July when soil started to dry up (Fig. 3). The same mechanism may also explain why we only found a significant decline in grass water content from T2 to T3 in the rain simulation experiment for the '25' tuft treatment and not for the '75' tuft treatment, while this was not found for the soil water content (Figs 6, 7). Therefore, the increased relative grass leaf water content with decreasing tuft cover in the post rain period, which again does not correspond with the soil water data, is a surprising observation since the reverse would be expected (Fig. 3). This higher grass leaf water content can however be explained by a greater availability of water per individual grass tuft, as there were less tufts present per unit area in the lower tuft cover treatments. Likewise the higher grass leaf N content in the lower tuft cover treatments can be explained.

The increased relative grass water content during the post-rain period, however, did not result in an increased production in plots with low tuft cover. The data therefore suggest that the greatest proportion of production occurred in the wet months. However, a significant higher LWR found at the end of the season in plots with low tuft cover (Fig. 4b) does suggest that plots with lower tuft cover can prolong their growth period into the dry season due to higher biomass of photosynthetically active leaf material.

Our study clearly demonstrates that removal of aboveground biomass affects soil water content and consequently vegetation production and nutrient content. The effect of removal of litter was more pronounced than that of tuft cover. Since fire removes both standing biomass and litter, while herbivores primarily remove standing biomass, our data suggest that the effect of fire on soil water content and subsequently vegetation production is more pronounced than the effect of herbivory.

Recent theoretical work has shown that when biomass reduction exceeds a certain threshold production may collapse as a consequence of reduced water infiltration (Rietkerk and Van de Koppel 1996, Chapter 3 in this thesis, Rietkerk et al. 1997, Chapter 4 in this thesis). In our study, reduction in production indeed occurred when a significant amount of aboveground biomass was removed. However, we found that this effect was mainly due to enhanced loss of soil water through evaporation when litter was removed, and not the consequence of reduced water infiltration.

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Chapter 6

Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system

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Submitted

Abstract

We studied the degree and scale of patchiness of vegetation and selected soil variables along a gradient of herbivore impact. The gradient consisted of a radial pattern of "high", "intermediate" and "low" herbivore impact around a watering point in a semi-arid environment in Burkina Faso (West Africa). We hypothesized that, at a certain range of herbivore impact, vegetated patches alternating with patches of bare soil would occur as a consequence of plant-soil feedbacks and run-off - run-on patterns. Indeed, our transect data collected along the gradient showed that vegetated patches with a scale of about 5-10 m, alternating with bare soil, occurred at intermediate herbivore impact. When analysing the data from the experimental sites along the gradient, however, we also found a high degree of patchiness of vegetation and soil variables in case of low and high herbivore impact. For low herbivore impact, most variation was spatially explained, up to 100% for vegetation biomass and soil temperature, with a patch scale of about 0.50 m. This was due to the presence of perennial grass tufts of *Cymbopogon schoenanthus*. Patterns of soil organic matter and NH_4-N were highly correlated with these patterns of biomass and soil temperature, up to r=0.7 ($p<0.05$) for the *in situ* correlation between biomass and NH_4-N. For high herbivore impact, we also found that most variation was spatially explained, up to 100% for biomass and soil temperature, and 84% for soil moisture, with three distinct scales of patchiness (about 0.50 m, 1.80 m and 2.80 m). Here, microrelief had a corresponding patchy stucture. For intermediate herbivore impact, again most variation was spatially explained, up to 100% for biomass and soil temperature, and 84% for soil moisture, with a patch scale of about 0.95 m. Here, we found evidence that vegetated patches positively affected soil moisture through less run-off and higher infiltration of rainwater that could not infiltrate into the bare soil elswhere, which was not due to microrelief. Thus, we conclude that our findings are in line with our initial hypothesis that, at intermediate herbivore impact, vegetated patches alternating with patches of bare soil persist in time due to positive plant-soil feedbacks.

Introduction

Several studies have shown that in semi-arid areas plant cover has major effects on soil resources and physical properties (Jackson and Caldwell 1993, Vinton and Burke 1995, Schlesinger et al. 1996). This indicates the possibility of feedbacks between plants and their micro-environment in these areas, such as positive feedbacks between plant cover and nutrient cycling, or between plant cover and infiltration of rain water (Schlesinger et al. 1990, Wedin and Tilman 1990, Vinton and Burke 1995). The importance of these plant-soil relations for ecosystem functioning lies in the potential for plant-induced soil changes to persist, as positive feedbacks are by definition self-reinforcing, and for yielding relatively high levels of primary productivity (Van Breemen 1993).

Overgrazing may disrupt these *in situ* plant-soil relations and create spatial heterogeneity (Schlesinger et al. 1990, 1996). Grazing and trampling by domestic livestock in semi-arid regions, concentrated around watering points and villages, often leads to a reduction of plant cover and to soil compaction. This causes rainfall running off instead of infiltrating into the soil (Elwell and Stocking 1976, Kelly and Walker 1976, Breman and De Wit 1983, Stroosnijder 1996), leading to spatial redistribution of soil moisture, erodable material and nutrients. The resulting spatial variation may be structured at certain scales, whereby vegetated patches concentrate soil water and nutrients lost from patches of bare, compacted soil (Schlesinger et al. 1990, Wilson and Agnew 1992, Ludwig and Tongway 1995).

Geostatistics are indispensable for analysing the degree and scale of spatial variation, and for comparing spatial patterns (Burrough 1995, Stein et al. 1997). Comparison of spatial patterns of vegetation and selected soil variables at a field scale has received little attention in ecological studies (but see Jackson and Caldwell 1993, Ryel et al. 1996). Comparison of such patterns may elucidate spatial relationships that were hitherto undemonstrated or unknown. In this study, we linked spatial patterns of different selected soil and vegetation variables, and analysed these links in relation to herbivore impact. We focussed on the conditions under which the spatial redistribution of soil resources and erodible material by run-off and run-on could lead to the formation and likely persistence of spatial patterns.

The first objective of our study was to investigate the degree and scale of patchiness (spatial autocorrelation) of vegetation and selected soil variables along a gradient of herbivore impact. The gradient in this study consisted of a radial pattern of herbivore impact around a 20-year old man-made watering point. Our second objective was to determine similarities between spatial vegetation and soil patterns along this gradient of herbivore impact.

We also measured the change in relative abundance of functional plant groups (e.g. annual and perennial grasses) along the gradient, and the effects of the main functional plant groups on some selected soil variables, given a certain herbivore impact. These effects were measured because the relative abundance of different functional plant groups changed with herbivore impact, and the effects of functional plant groups and herbivore impact on selected soil variables consequently interact (Vinton and Burke 1995). It was not our aim to elucidate mechanistically how grazing and trampling affected the different functional groups and the interaction between those groups.

Herbivore impact in dry areas is typically focussed around livestock watering points (Valentin 1985, Andrew 1988). Therefore, we refer to the zone closely encircling the watering point we selected as being exposed to "high" herbivore impact. Further, intense grazing and trampling around foci of herbivore impact generally result in bare, compacted soil stripped from any vegetation (Valentin 1985, Andrew 1988). Thus, at high herbivore impact we expected a relatively homogenous soil with no vegetation patchiness.

We refer to the zone far off from the watering point where the intensity of livestock trails is low and herbivores rarely wander as being exposed to "low" herbivore impact. We hypothesized that, at low herbivore impact, the degree of patchiness would be relatively low, and that scales of patchiness could be attributed to differences in *in situ* effects that functional plant groups have on soil resources and physical properties (Jackson and Caldwell 1993, Vinton and Burke 1995, Schlesinger et al. 1996).

We refer to the zone between the zones of high and low herbivore impact as being exposed to "intermediate" herbivore impact. Note the ordinal nature of the scale. Further, note that in theory, when the spatial pattern of herbivore impact depends on the location of the watering point only, zones with equal herbivore impact surrounding the watering point should be concentric, but this is in reality not the case. At intermediate herbivore impact, it was hypothesized that the degree and scale of patchiness would be relatively high as patches of bare, crusted and compacted soil could cause run-off of water and erodable material. Resources could subsequently become available for vegetated patches because of run-on. The rationale behind this hypothesis was derived from Rietkerk and Van de Koppel (1997) (Chapter 3 in this thesis) and Rietkerk et al. (1997) (Chapter 4 in this thesis). Their theoretical models showed that within certain ranges of herbivore impact small initial differences in plant cover and amount of soil resources can magnify to alternative states that persist in time due to positive plant-soil feedbacks.

Material and methods

Field sampling and laboratory analysis

Site description

Fieldwork was carried out in Burkina Faso (West Africa) from June - September 1996 and the same period in 1997 near the village of Kaibo Sud V6 (11°7'N, 0°9'W), approximately 100 km south-east of the capital Ouagadougou. Average annual rainfall is 800-900 mm (North Sudanian ecoclimatic zone); the rainy season lasts from May - September. Average annual temperature is 28°C. Physiographically the area can be classified as a moderately high plateau with hills and rock outcrops. The moderately deep (40-80 cm) to deep (>80 cm) soils of the area are mainly Eutric Regosols (75%) and Eutric Leptosols (18%). Landcover varies from tree savanna of low to medium (2-10%) coverage of trees and low (10-25%) coverage of agricultural fields, to medium (5-10%) coverage of trees and high (>70%) agricultural field coverage around the villages (Mulders 1996). The (semi-)natural vegetation shows a high (10-20%) coverage of shrubs and low trees with an understorey of the perennial grass *Cymbopogon schoenanthus* (L.) Spreng. and annual grasses and herbs. It is extensively grazed by cattle from the Mossi and the Fulani for about 20 years, since the area was recolonized after eradication of onchocerciasis (river blindness).

For this study a grazing area with a watering point was selected, where herbivore impact (grazing and trampling) diminished radially with distance from the watering point. The watering point consisted of a 20-year old waterpump at the southern edge of the village where spoiled water used for households is collected in a trough enabling livestock to drink. The research site was only gently sloping at 2-3%.

Transects

To verify an underlying gradient of herbivore impact five transects of approximately 200 m were laid out radial from the watering point. Faeces countings were carried out in series of 10*10 m quadrats laid out over each transect with the underlying assumption that the accumulation of faeces correlates with the animal time spent there. The transects were used as axes of the series of quadrats, and for the design of the quadrats consecutive tracts of 10 m of the transect itself and 5 m at each side of the transect were used. In each of these quadrats the total number of faecal droppings were counted.

Further, vegetation height (cm) and type of functional plant group (perennial grasses, perennial herbs, annual grasses and annual herbs) and the occurrence of bare ground and litter were recorded at 0.1 m intervals along two (Transect 1 and 2) of the five transects. This was not done for the remaining three transects because of the occurrence of human tracks and other disturbances which we avoided. Transect 1 consisted of 1836 sampling points (183.5 m long) and transect 2 of 2301 sampling points (230.0 m long). Vegetation height was measured by lowering a perforated foam disc (diameter 0.1 m, weight 7 g) onto the vegetation along a gauged stick. All these measurements took place at the end of July 1996.

Soil variables in relation to functional plant groups

The dominant functional plant groups were perennial grasses and annual grasses. To investigate the effect of these plant groups on different soil variables, an area of approximately 15*15 m was fenced. Within this exclosure, a total of 15 plots of 0.25*0.25 m were selected, 5 replicates for each functional plant group and 5 plots with bare ground. Within a scale of 0.25*0.25 m annual grasses almost always co-occurred with annual herbs, but these plots are referred to as annual grasses anyway. Aboveground biomass was removed before soil sampling. Samples of the upper 8 cm of the soil were taken at each plot to determine soil moisture content, organic matter content and soil texture. Soil moisture content (weight % on basis of oven-dry soil) was determined gravimetrically, organic matter content (weight % on basis of oven-dry soil) by loss on ignition and soil texture (weight % on basis of oven-dry soil) by sieve and pipette. Bulk density (g cm^{-3}) was determined by taking undisturbed samples of 100 cm^3 and placing them in an oven at 105^0C until constant weight was reached. Water infiltration (ml min^{-1}) on 0.25*0.25 m plots was measured using a small rainfall simulator (Kamphorst 1987, Eijkelkamp Agrisearch Equipment). Water infiltration was calculated by subtracting run-off from simulated rainfall. Each simulation consisted of a rain shower with a duration of 3 min and an intensity of 6 mm min^{-1} (375 ml min^{-1} on 0.25*0.25 m plots). These measurements took place in July 1996.

Additionally, in July 1997, infiltration capacity (ml min^{-1}) on 0.25*0.25 m plots with different aerial vegetation cover of perennial grasses and annual grasses was measured. Theoretically, with a constant rainfall, infiltration decreases asymptotically to a certain final constant value as time increases (Stroosnijder 1976, Kiepe 1995). This time each measurement was repeated untill run-off was constant and at its maximum, so that final constant infiltration (infiltration capacity) could be calculated. Each measurement consisted of a rain shower of 4-5 min with a constant intensity of 6 mm min^{-1}. Two series of measurements were performed, for plots with annual grasses only (in the absence of perennial grass tufts), and for plots including perennial grass tufts. Before the measurements, these tufts were cut till about 5 cm height for practical reasons. The coverage of perennial grasses, annual grasses, litter and bare ground was estimated using a square quadrat with 10*10 subdivisions.

Experimental sites

Three sites (A, B and C) were selected which differed in herbivore impact because of their relative distance from the watering point and the nearby village; the longer these distances, the lower the herbivore impact. Herbivore impact was high for site A, intermediate for site B and low for site C. At each site, a 7*5 matrix of 35 sampling points was established at 1 m interspaces. At each of these so-called base points two additional sampling points were located in a randomly assigned direction (N, NE, E, SE, S, SW, W, NW), at 0.2 and 0.4 m from each base point (Gross et al. 1995). This resulted in a total of 105 sampling points per site (315 in total) in a stratified-nested design. The three sites were fenced to prevent people and livestock from disturbing the sites during the experimental measurements.

Soil and vegetation measurements at the sites

Run-off - run-on patterns were quantified by randomly scattering coloured plastic beads (available at local markets) over the sites and measuring their spatial distribution before and after rainfall. This was done by counting the number of beads on a 1 dm^2 surface at each sampling point, directly after scattering and after rainfall. On July 9 1997, 8400 beads of type 1 and 650 beads of type 2 were scattered per site, counted, and recounted on July 15 1997 after 51.4 mm of rain with a duration of 237 min. Type 1 beads were round, with an average diameter of 4.0 mm and an average weight of 0.026 g. Type 2 beads were oval shaped, on average 9.0 mm long, with an average diameter of 5.0 mm and an average weight of 0.109 g.

To quantify microrelief within each site, the height differences between all sampling points were measured by a using a surveyor's level and levelling staff with an accuracy of 1 mm. Thus, the relative altitude (mm) of all sampling points with respect to one imaginary zero level was known. Soil moisture content (vol %) was measured with the Trime TDR (Time Domain Reflectometry) measurement system (Eijkelkamp Agrisearch Equipment) at 5 cm soil depth on July 15 1997, 12-16 hours after a rainshower of 31.4 mm with a duration of 201 min. Soil temperature (°C) was measured on July 16 1997, at midday and 34-38 hours after the same shower, with an electronic soil thermometer at 2.5 cm soil depth. Penetrability (kN) was measured on July 23 1997, 37-41 hours after a rain shower of 6.2 mm with a duration of 32 min, with a soil penetrometer as a measure of top soil compaction and crust formation. Ideally, all these highly fluctuating variables should be measured at the same time, but due to practical reasons (e.g. the large number of sampling points and instruments that could only measure within certain ranges of soil moisture content) this was not possible. Care was taken to minimize sampling time per measuring series.

At the end of July 1997, at each sampling point the aboveground biomass (g dm^{-2}) of 1 dm^2 was harvested, air dried, sorted into different functional plant groups (annual grasses, annual herbs, perennial grasses, perennial herbs) and litter, and weighed with an electronic balance. Prior to harvesting, the height of the vegetation (cm) was measured, and aerial coverage (%) of annuals, perennials, litter and bare ground for each sampling point of 1 dm^2 was estimated using a square quadrat with 4*4 subdivisions.

Finally, after sampling the aboveground biomass, a soil core of 5 cm diameter was taken at each sampling point at 0-5 cm depth. The soil samples were put in small plastic bags and air dried. In the laboratory, the air dried samples were sieved with a 2 mm sieve. Per sample, two subsamples were taken of approximately 30 g, one for determining particle size distibution and one for chemical analysis. Particle size distribution was measured by laser diffraction using a Coulter LS230 Particle Size Analyser (Coulter Electronics Ltd.) that is able to determine the volume percentage of 116 particle size classes between 0.040 and 2000 μm (Buurman et al. 1997). As variable for further analysis the volume percentage of 1-100 μm was used, based on the characteristic differential volume curves derived from each sample. Before measuring, the samples were treated with a 300 g l^{-1} hydrogen peroxide (H_2O_2) solution and 3 min ultrasound to eliminate the effects of aggregation by soil organic matter. Organic matter content (weight % on basis of oven-dry soil) was determined by loss on ignition. Available PO_4-P, NO_3-N and NH_4-N (mg kg^{-1}), were determined with an auto-analyser after extraction with 0.01 M calciumchloride ($CaCl_2$).

Statistical analysis

Transects

Linear regression analysis was carried out to explore the relationships between distance from the watering point and the number of faecal droppings counted in the quadrats along the different transects. Moving averages of vegetation height and moving relative abundance of functional plant groups (n=100) along transect 1 and 2 were calculated for a graphical exploration of the transect data. The spatial variation of vegetation height along transect 1 and 2 was evaluated by semivariance analysis, which analyses the variance between measurements taken at increasing distance from each other (Burrough 1995, Robertson and Gross 1994). The semivariance γ for a certain distance interval h is calculated as half the average of squared differences of pairs of observations for which the distance between the observations falls within that interval:

$$\gamma(h)=\frac{1}{2*N(h)}\sum_{i=1}^{N(h)}[y(x_i)-y(x_i+h)]^2 \tag{1}$$

where $N(h)$ is the total number of pairs that are separated by distance interval h, and $y(x_i+h)$ is the value of a variable at a distance interval h from x_i (Burrough 1995, Robertson and Gross 1994). Multiple spatial resolutions (minimum distance intervals) varying from 0.1 m to 2.0 m were used to optimally analyse different scales of patchiness.

Common models (Robertson et al. 1988, Jackson and Caldwell 1993, Schlesinger et al. 1996, Robertson et al. 1997) were used in order of increasing complexity to fit the form of the semivariograms. In the linear model with a sill, $\gamma(h) = C_0+(C_1/A_1)h$ if $h<A_1$, and $\gamma = C_0+C_1$ if $h>A_1$, where γ is the semivariance, h is the lag, A_1 is the range, C_0 is the nugget variance, and C_1 the structural variance. In the spherical model, $\gamma(h) = C_0+C_1[1.5(h/A_1)-0.5(h/A_1)^3]$ if $h<A_1$, and $\gamma = C_0+C_1$ if $h>A_1$. In the two-level Gaussian model, $\gamma(h) = C_0+C_1[1-\exp(-1\{h^2/A_1^2\})]$ if $h<q_1$, and $\gamma(h) = [C_0+C_1]+C_2[1-\exp(-1\{[h-q_1]^2/A_2^2\})]$ if $h>q_1$, where q_1 is the transition point from semivariogram 1 to semivariogram 2, C_2 is the structural variance of semivariogram 2, and A_2 the range of semivariogram 2. In the three-level Gaussian model, a third semivariogram could be distinguished. Thus, $\gamma(h) = [C_0+C_1+C_2]+C_3[1-\exp(-1\{[h-q_2]^2/A_3^2\})]$ if $h>q_2$, where q_2 is the transition point from semivariogram 2 to semivariogram 3, C_3 the structural variance of semivariogram 3, and A_3 the range of semivariogram 3. The proportion of the total variance accounted for by structural or spatially dependent variance is calculated by $C_1/(C_0+C_1)$ in case of a one-level model (linear model with a sill or spherical model). In case of a two-level and three-level model the proportion structural variation is calculated by $(C_1+C_2)/(C_0+C_1+C_2)$ and $(C_1+C_2+C_3)/(C_0+C_1+C_2+C_3)$, respectively. The simplest model with the highest R^2 was considered as optimal. A more complex model was choosen if its R^2 was at least 0.05 higher than the R^2 of a less complex one. If according to this standard procedure the optimal model was a linear model, then this model was only choosen if its $p<0.05$. If $p>0.05$, then the random model was considered appropriate.

Soil variables in relation to functional plant groups

Soil variables as measured for the 0.25*0.25 m plots (texture, organic matter content, soil moisture content, bulk density and infiltration) were compared pairwise between bare soil, annual grasses and perennial grasses using the Mann-Whitney U test. Linear regression analysis was performed to test the dependence of infiltration capacity on aerial cover of annual grasses and perennial grasses respectively.

Soil and vegetation measurements at the sites

Site means were compared pairwise using the Mann-Whitney U test. The magnitude of within-site variability was evaluated by comparing coefficients of variation (%). To explore the correlation structure of the data set, Principal Component Analysis (PCA) was used. PCA reduces the original amount of variables to a few components representing sets of correlated variables. Further analysis and discussion was mainly focussed on the variables with the highest eigenvectors for the first component.

The spatial variation of the variables was evaluated by calculating the semivariograms and fitting optimal models (the best fitting equation), as was done for vegetation height along the two transects. For each variable of the three sites, the lag interval evaluated was 0-4 m (approximately half the maximum distance between sampling points) with a spatial resolution (minimum distance interval) of 0.2 m. The cross-correlogram was used to compare spatial patterns of especially those variables with the highest eigenvectors for the first component. The cross-correlogram plots the cross-correlation $r_{ab}(h)$ between two variables as a function of the distance interval h between sampling points. To calculate $r_{ab}(h)$ from available data, consider pairs of observations $a(x_i)$ and $b(x_i+h)$, separated by distance interval h. For $N(h)$ pairs of observations, $r_{ab}(h)$ is calculated as:

$$r_{ab}(h) = \frac{\sum_{i=1}^{N(h)} a(x_i)b(x_i+h) - m_a m_b}{s_a s_b} \qquad (2)$$

where m_a and m_b and s_a and s_b denote sample mean and standard deviation of a and b respectively (Stein et al. 1997). If patterns are completely similar and overlapping, $r_{ab}(0)$ is equal to 1; if patterns are completely opposite and overlapping, $r_{ab}(0)$ is equal to -1. Commonly, the cross-correlation gradually shifts towards zero for increasing values of h, indicating a range of spatial dependence. For totally unrelated patterns, $r_{ab}(h)$ equals zero. If patterns show similarities for certain distances larger than zero, $r_{ab}(h)$ may show a peak for those specific distances.

Linear trends and data transformation

If significant ($p<0.01$) linear trend lines or trend surfaces were present for the variables evaluated, the given variables were represented by the deviations from the trends for the geostatistical analyses, as well as for the PCA. This was the case for most of the variables. This caused most (detrended) variables to approach a normal distribution. Therefore, and because unbiased comparisons of scales of patchiness between variables and between sites were needed, data were not transformed. For comparisons between means, non-parametric tests were used.

Results

Transects

The average number of faecal droppings of the five transects showed a significant ($p<0.001$) decrease with increasing distance. Therefore, the assumption of an underlying gradient of herbivore impact radial to this watering point was justified. For transect 1 a significant decrease in the number of faecal droppings with increasing distance from the water point was found ($p<0.001$), but not for transect 2 (Fig. 1). For both transects, vegetation height generally increased with increasing distance from the watering point (linear regression, $p<0.01$), while the moving relative abundance ($n=100$) of bare soil decreased. At an intermediate distance from the watering point, the moving average of vegetation height ($n=100$) as well as the moving relative abundance of annual and perennial grasses showed a clear periodic signal for transect 1 with the underlying gradient of herbivore impact, but not for transect 2, which did not show a significant gradient.

For transect 1 four different scales of patchiness emerged while for transect 2 two scales of patchiness were found (Fig. 2). For both transects the smallest scale of patchiness (about 0.75 m) consisted of perennial grass tufts (Figs 2a, d; see Table 1 for parameter values of optimal models). The proportion structural variance ($C_1/[C_0+C_1]$) analysed at this scale was 1.00 for transect 1 and 0.96 for transect 2. The next scale of patchiness of about 5-10 m (Figs 2b, e) consisted of vegetation patches of co-occurring annuals and perennials alternating with bare soil. Two additional scales of patchiness were recognized for transect 1 (Fig. 2c), representing relatively homogeneous parts of the transect (bare soil close to the watering point and a continuous vegetation cover at the end of the transect), and the remaining intermediate part where the periodic signal occurred. The periodicity of this signal can be recognized by the cyclic pattern in the semivariogram. Analysed at a lag interval of 0-100 m, transect 2 was optimally fitted by a linear model without a sill (Fig. 2f), indicating increasing deviations from the linear trend with increasing distance interval.

It should be noted that the range parameters obtained by the nested Gaussian model fitting are smaller as compared to the ranges if estimated by eye. This difference is due to the asymptotic character of the sigmoid curve. Therefore, patch sizes obtained by the nested Gaussian model fitting could probably be better estimated by eye.

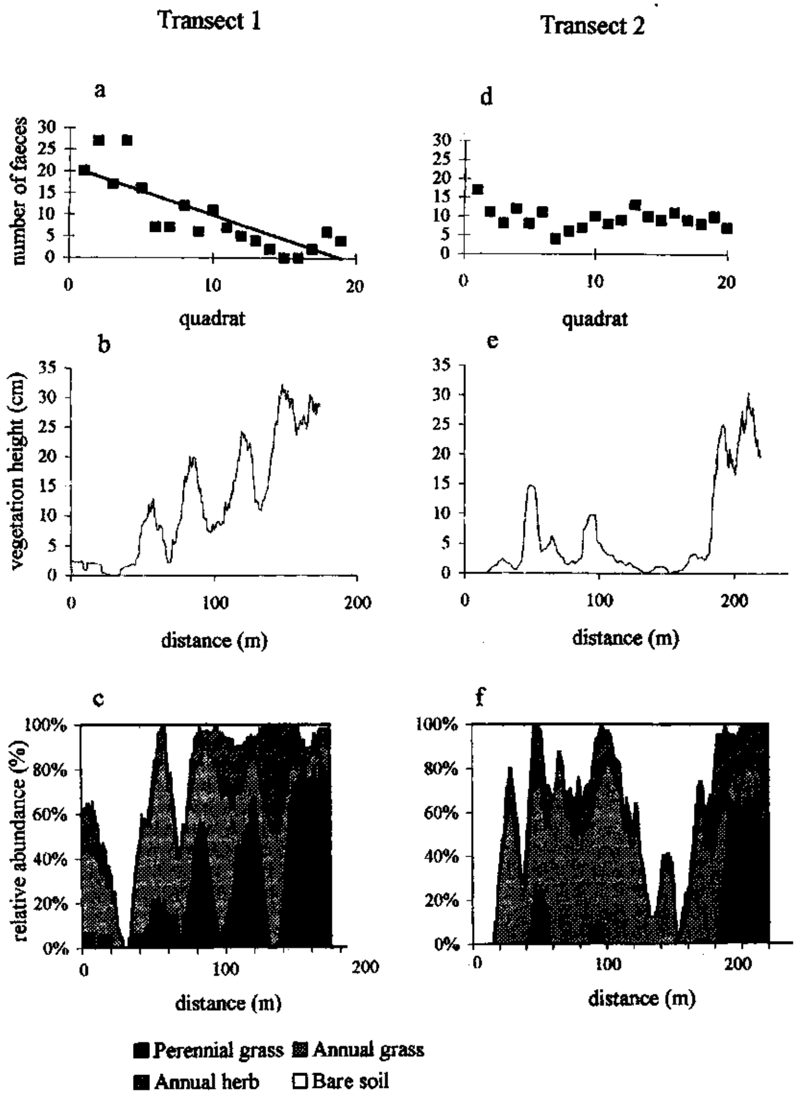

Fig. 1. Results of transects 1 (a-c) and 2 (d-f). (a, d) Number of faecal droppings as a function of quadrat number (which equals distance from watering point if multiplied by 10) (linear regression transect 1: $p<0.001$, $R^2=0.64$; linear regression transect 2: not significant). (b, e) Moving average (n=100) of vegetation height. (c, f) Moving relative abundance (n=100) of bare soil, annual herbs, annual grasses and perennial grasses.

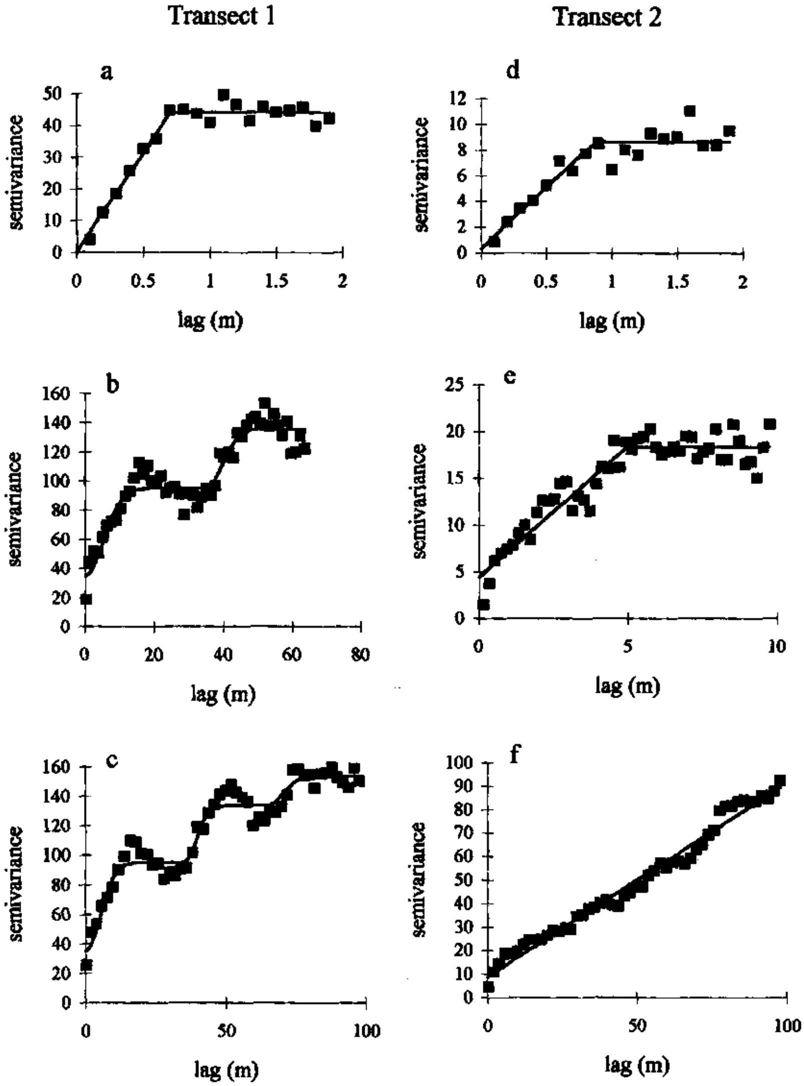

Fig. 2. (a-f) Semivariograms for vegetation height (cm) of transect 1 and 2 for different lag intervals. Maximum lag interval was 0-100 m, approximately half the length of the transects. For parameters of optimal models, see Table 1.

Table 1. Parameters of the optimal models of the transect semivariograms of vegetation height. In order of increasing complexity the models we have tested were: linear model (=linear), linear model with a sill (=sill), and spherical model (=spher). If appropriate, a two-level or three-level Gaussian model (=gauss) was applied. The parameters C_0, C_1, C_2, C_3, A_1, A_2, A_3, q_1 and q_2 are explained in the text.

Transect	**Lag interval (m)**	**Model**	R^2	C_0	C_1	**proportion structured variance**	A_1 **(m)**	C_2	A_2 **(m)**	C_3	A_3 **(m)**	q_1 **(m)**	q_2 **(m)**
Transect 1	0-2	sill	0.97	0.00	44.15	1.00	0.71	-	-	-	-	-	-
Transect 1	0-65	gauss	0.91	34.92	60.24	0.74	7.48	40.44	6.32	-	-	35.16	-
Transect 1	0-100	gauss	0.95	34.89	60.11	0.77	7.48	38.59	6.13	19.71	7.48	35.00	65.00
Transect 2	0-2	sill	0.88	0.33	8.30	0.96	0.87	-	-	-	-	-	-
Transect 2	0-10	sill	0.90	4.43	13.92	0.76	4.99	-	-	-	-	-	-
Transect 2	0-100	linear	0.98	8.70	-	-	-	-	-	-	-	-	-

As significant linear trends ($p<0.01$) were present in the data evaluated, the given data was represented by the deviations from the trend before calculation of the semivariograms.

Soil variables in relation to functional plant groups

Soil organic matter and moisture was significantly higher in vegetated plots than in bare soil plots (Table 2). Bulk density of bare soil was significantly higher than in perennial grass plots. Infiltration significantly increased from bare soil plots to annual grass plots, and from annual grass plots to perennial grass plots. Soil samples taken from annual grass plots contained significanty more clay and less sand than samples taken from bare soil plots. Infiltration capacity increased both with increasing annual grass cover and perennial grass cover (linear regression, $p<0.05$) (Fig. 3). The slope of the regression line was more steep in case of increasing perennial grass cover than in case of increasing annual cover in the absence of perennials. Given a certain aerial vegetation cover, plots with perennial grass have a higher infiltration capacity than plots with annual grass.

Table 2. Mean values of soil variables for different functional plant groups and bare soil, and number of observations (n). Significant differences between means (Mann-Whitney U test, $P<0.05$) are indicated by different letters.

Variable	Mean (n)		
	Bare soil	Annual grass	Perennial grass
soil moisture (%)	10.76 (5) a	14.30 (5) b	15.72 (5) b
soil organic matter (%)	1.32 (10) a	1.95 (10) b	2.11 (10) b
bulk density (g cm^{-3})	1.62 (5) b	1.55 (5) ab	1.36 (5) a
infiltration (ml min^{-1})	158 (5) a	262 (5) b	>375 (5) c
clay (%)	34 (8) a	40 (8) b	40 (8) ab
loam (%)	31 (8) a	29 (8) a	28 (8) a
sand (%)	35 (8) a	31 (8) b	32 (8) ab

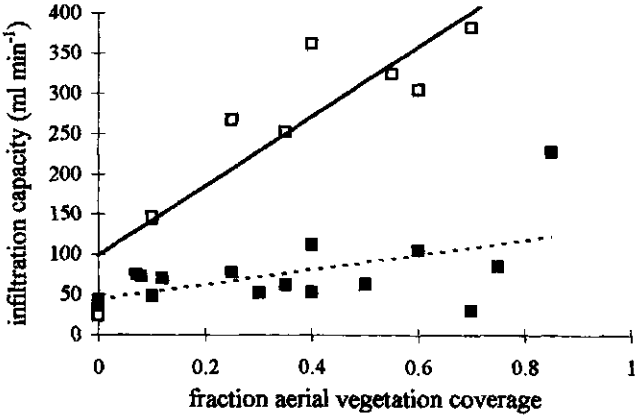

Fig. 3. Linear regression between infiltration capacity on 0.25*0.25 m plots and annual grass coverage (■) ($p<0.05$, $R^2=0.30$) and perennial grass coverage (□) ($p<0.001$, $R^2=0.81$). For the measurement series of annual grass coverage, vegetation cover consisted only of annual grasses. For the measurement series of perennial grass coverage, vegetation cover consisted of perennial grass as well as annual grasses and litter, but only perennial grass coverage was used in the regression analysis.

Variation between and within sites

The amount of beads found after rainfall indicated that run-off was higher for site A and site B as compared to site C (Table 3). Due to the gentle undulation of the research area, site B was situated about 40 cm lower than site A and C. Mean biomass, aerial biomass cover, vegetation height, soil moisture and available PO_4-P (n=105) increased significantly from site A (high herbivore impact) to site B (intermediate herbivore impact), and from site B to site C (low herbivore impact). Site A and B were characterized by an absence of perennial vegetation and litter, the vegetation only consisted of annuals. In site C, average aerial cover of perennials (mainly grass tufts of *Cymbopogon schoenanthus*) was about 14% and that of litter was about 19%. NH_4-N was about two to three times higher in site C than in site A and B. NO_3-N was about four times higher in site B than in site A and C. Soil organic matter in site B and C was significantly higher than in site A. Soil compaction and soil temperature of the top soil was lowest in site C. Soil texture differed significantly between the sites; volume % of soil particle diameter from 1-100 µm was highest for site B and lowest for site C. The coefficients of variation associated with the mean values (n=105) (Table 3) offer an index of the overall variation of vegetation and soil variables within each site. Coefficients of variation were generally low for altitude, soil temperature, soil organic matter and texture (<20%). Higher coefficients of variation were found for vegetation height, soil moisture, NO_3-N and penetrability (approximately 20-100%). Coefficients of variation higher than 100% were found for the other variables. High coefficients of variation were especially found for amount of beads and PO_4-P in site A. Site C had a very high coefficient of variation for NH_4-N. Site B had the lowest coefficients of variation, except for aerial biomass cover, amount of beads, penetrability and soil temperature.

Correlation structure

For all sites, four principal components together contributed for more than 65% in explaining the total variation in the data (%Var Component [I + II + III + IV], Table 4). Component I contributed relatively much in explaining these variation, 29.2%, 32.1% and 31.6% for site A, B and C respectively. For site A and B the highest weightings for this component were soil temperature, biomass, soil moisture, amount of beads and penetrability. This means that these variables were more or less correlated for these sites and that together they are relatively important in explaining the total variation in the data. Thus, in site A and B, higher biomass, higher soil moisture and less run-off were associated with lower soil temperature and less soil compaction. In site C, soil moisture, run-off and penetrability did not contribute to component I; the highest eigenvectors for this component were biomass, NH_4-N, soil organic matter, soil temperature and altitude. Thus, in site C, higher biomass, higher soil organic matter and higher NH_4-N were associated with micro-elevations and lower soil temperatures. This can be understood by the presence of perennial grass tufts in this site, which consist of micro-elevations through the accu-

Table 3. Mean values and coefficients of variation (sd/mean x 100%) of 105 sampling points. Significant differences between means (Mann-Whitney U test, $p<0.05$) are indicated by different letters.

Variable	High herbivore impact		Intermediate herbivore impact		Low herbivore impact	
	Site A		Site B		Site C	
	Mean	CV(%)	Mean	CV(%)	Mean	CV(%)
Number of beads before rain (dm^{-2})	3.21 a	104.8	3.77 b	71.2	2.27 a	104.1
Number of beads after rain (dm^{-2})	0.62 a	268.2	0.49 a	233.9	2.16 b	147.3
Relative altitude (mm)	-1110.76 b	2.2	-1519.39 a	1.1	-1115.92 b	2.4
Biomass ($g\ dm^{-2}$)	0.48 a	150.2	0.69 b	93.0	6.18 c	166.2
Biomass cover (%)	15.17 a	144.0	23.67 b	101.8	76.22 c	35.9
Vegetation height (cm)	3.70 a	68.2	5.18 b	68.0	21.56 c	79.7
Soil moisture (vol. %)	5.59 a	40.3	6.30 b	23.4	8.52 c	35.3
Soil temperature (°C)	41.47 b	5.8	42.07 c	7.1	33.10 a	7.4
Soil organic matter (%)	2.67 a	13.8	3.80 b	11.8	3.99 b	17.8
NH4-N ($mg\ kg^{-1}$)	1.37 a	69.9	1.34 a	68.2	3.76 b	155.9
NO3-N ($mg\ kg^{-1}$)	3.25 a	102.3	13.20 c	66.7	3.76 b	73.2
PO4-P ($mg\ kg^{-1}$)	$9.52.10^{-3}$ a	371.9	$98.76.10^{-3}$ b	117.9	$106.57.10^{-3}$ c	179.5
Penetrability (kN)	0.11 b	38.8	0.11 b	44.9	0.05 a	68.3
Texture (vol. % 1-100 μm)	51.28 a	13.3	77.42 c	6.5	60.17 b	11.5

Table 4. Eigenvalues, percentages of variation (%Var) explained and eigenvectors of variables for each component (Comp) and each site, evaluated by PCA. Bold values indicate highest eigenvector scores for a given variable.

Site	Parameter PCA	Variable	Comp I	Comp II	Comp III	Comp IV
A	Eigenvalue		3.22	1.56	1.32	1.13
	%Var		29.2	14.2	12.0	10.2
	Eigenvector	Soil temperature*	**-0.86**	0.08	-0.05	0.35
		Biomass*	**0.83**	-0.04	-0.05	0.19
		Soil moisture*	**0.77**	0.08	-0.03	-0.36
		Penetrability*	**-0.65**	-0.39	0.11	0.15
		Beads*	**0.50**	-0.48	0.19	0.42
		Soil organic matter	0.43	**0.60**	0.31	0.11
		PO_4-P*	-0.33	**0.51**	-0.04	0.09
		Texture*	-0.19	0.50	**0.61**	0.16
		NH_4-N	0.20	-0.41	**0.65**	0.25
		Altitude*	-0.28	-0.10	0.60	**-0.63**
		NO_3-N	0.25	0.33	0.00	**0.35**
B	Eigenvalue		3.53	1.53	1.25	1.10
	%Var		32.1	13.9	11.3	10.0
	Eigenvector	Soil temperature*	**-0.91**	0.10	0.09	0.19
		Biomass*	**0.83**	-0.22	0.06	-0.10
		Soil moisture*	**0.75**	-0.17	-0.21	-0.20
		Penetrability	**-0.72**	-0.16	-0.01	-0.05
		Soil organic matter*	**0.72**	0.44	0.01	0.03
		Beads	**0.46**	-0.19	0.32	0.37
		PO_4-P*	0.20	**0.64**	0.44	-0.27
		NH_4-N*	-0.25	0.23	**0.62**	-0.45
		Altitude*	-0.11	-0.45	**0.51**	0.16
		Texture*	-0.30	0.45	**-0.49**	-0.16
		NO_3-N	0.12	0.55	0.09	**0.73**
C	Eigenvalue		3.47	2.02	1.26	1.06
	%Var		31.6	18.4	11.4	9.6
	Eigenvector	NH_4-N*	**0.86**	-0.11	0.06	-0.18
		Biomass	**0.85**	0.09	0.24	-0.02
		Soil organic matter	**0.78**	0.06	0.14	0.20
		Soil temperature*	**-0.68**	0.48	0.21	-0.16
		Altitude*	**0.61**	0.49	-0.24	0.25
		Texture*	-0.12	**-0.77**	0.13	-0.10
		Penetrability	-0.53	**0.62**	0.29	-0.17
		Soil moisture*	-0.02	-0.51	**0.56**	-0.15
		NO_3-N	0.09	0.36	**0.59**	0.49
		Beads	-0.30	-0.31	0.37	**0.50**
		PO_4-P	0.41	0.24	0.41	**-0.59**

If significant linear trend surfaces ($p<0.01$) were present in the variables evaluated, the given variables (indicated by *) were represented by the deviations from the trend surface before evaluations by PCA.

mulation of organic material. Soil organic matter became increasingly important with decreasing herbivore impact (going from site A to site B to site C). Cross-correlograms shed a more detailed light on the correlations between variables for the different sites (see section Cross-correlograms).

Semivariograms

Beads showed a more or less patchy distribution after scattering (Fig. 4 and Table 5). Heavy and intense rain (51.4 mm with a total duration of 237 min) caused severe run-off from site A and site B. Most beads were washed away from these two sites (Table 3), leading to low semivariances and leaving no robust spatial structures within these sites after the rain. Note the similarity of the two semivariograms of the amount of beads before and after rain for site C, indicating no spatial redistribution for this site.

For each site, the semivariograms of biomass, soil temperature and soil moisture showed similar scales of patchiness, except for the semivariogram of soil moisture at site C (Figs 5b, c, d and Table 5). Note that for site A the optimal model fitted through the semivariograms of biomass, soil temperature and soil moisture was a three-level Gaussian curve, indicating three distinct levels of spatial structure at this site. For site B the semivariograms of these variables showed a clear range (A_l) of about 1 m. For site C this range was much smaller, but not for soil moisture which did not have a clear patchy structure at this site. For each site, nugget variance (C_0) was zero (and proportion structured variance was 1.00) for biomass and soil temperature, meaning that for these variables no additional spatially determined variance was present for distances smaller than the minimum lag distance of 0.20 m. The semivariograms of altitude showed a relatively large scale of patchiness (A_l=2.89 m) for site A, a smaller scale for site B and no clear patchy structure for site C (Fig. 5a). Note the high R^2 (0.99) of the linear model with a sill for this variable for site A (Table 5). Interestingly, also a three-level Gaussian curve accurately fitted the altitude semivariance data for this site, its R^2 was only 0.01 lower (0.98) than that of the optimal model. So, semivariograms of altitude, biomass, soil moisture and temperature showed a corresponding patchy structure for site A. Semivariances of altitude, biomass and soil moisture were relatively high for site C as compared to the other sites.

Soil organic matter showed a comparable proportion structured variance for the three sites, and the scale of patchiness was relatively small for site A as compared to site B and C (Fig. 5e). NH_4-N showed a more or less similar patchy structure for site A and B, but for site C no clear sill could be detected (Fig. 5f). Semivariances of both soil organic matter and NH_4-N were higher at site C as compared to the other sites. For NO_3-N no clear patchiness could be distinguished. The semivariogram of PO_4-P only showed a sill for site B, but the nugget variance was relatively high. Penetrability showed a more or less similar patchy structure for all sites. The semivariogram of soil texture did not show a sill for site B, but for site A and C a clear patchy structure could be recognized, whereby site A had the highest proportion of structured variance (Table 5).

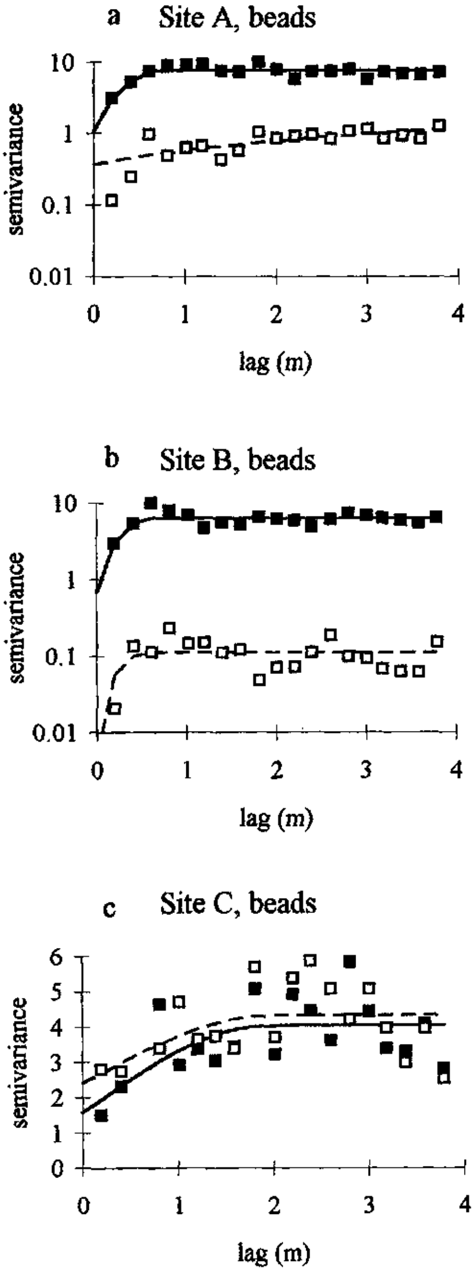

Fig. 4. (a-c) Semivariograms of amount of beads counted before rain (■) and after rain (□) for each site. Lines represent optimal models. For parameters and types of optimal models, see Table 5. A log semivariance scale is used if semivariances of the amount of beads showed large differences between observations before and after rain.

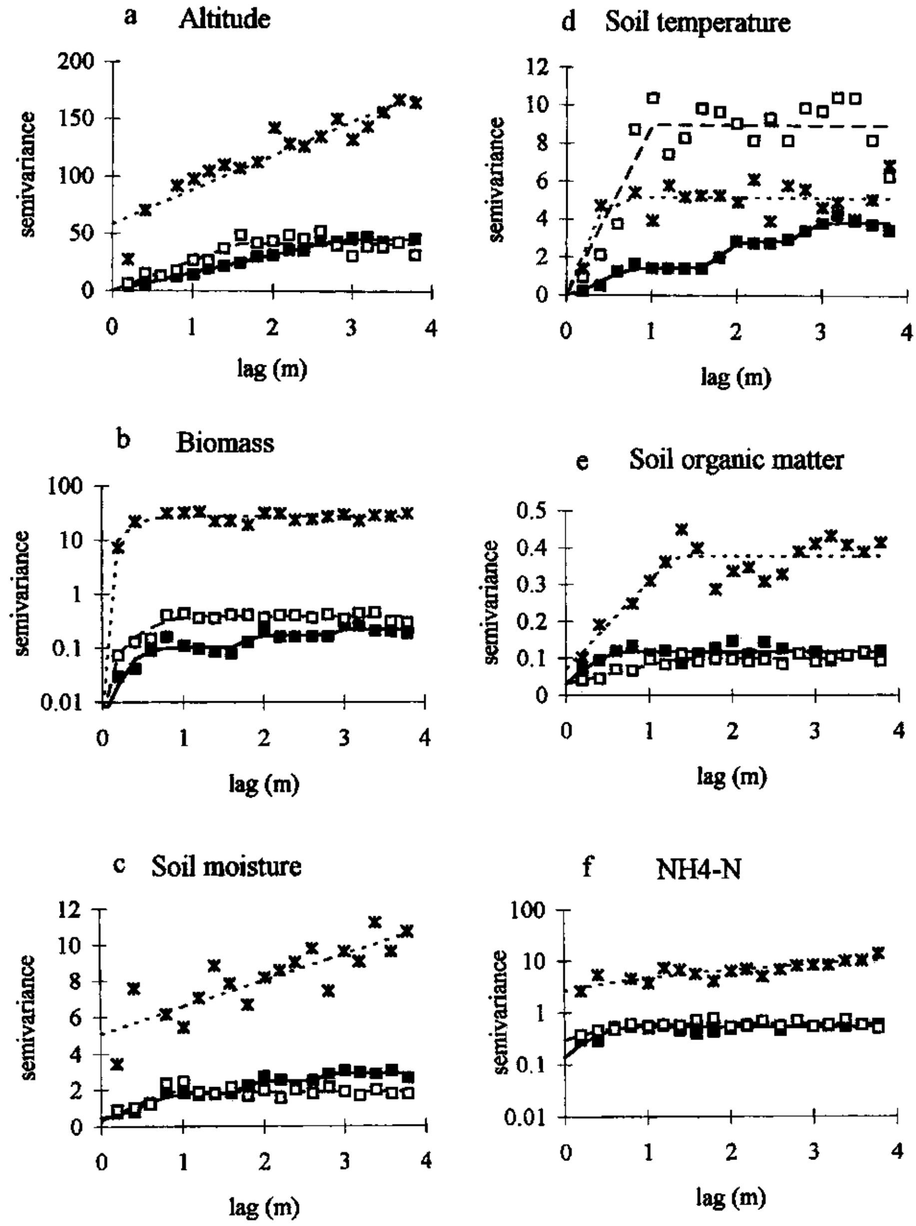

Fig. 5. Semivariograms of the most important variables (according to PCA) (a) altitude, (b) biomass, (c) soil moisture, (d) soil temperature, (e) soil organic matter and (f) NH_4-N for site A (■), B (□) and C (*). Lines represent optimal models. For parameters and types of optimal models for all variables, see Table 5. A log semivariance scale is used if semivariances of certain variables showed large differences between sites.

Table 5. Parameters of the optimal model of the semivariograms. In order of increasing complexity the models we have tested were: random model (=rand), linear model (=linear), linear model with a sill (=sill), and spherical model (=spher). If appropriate, a three-level Gaussian model (=gauss) was applied. Minimum distance interval: 0.2 m; number of lags: 20; lag interval: 0-4 m. The parameters C_0, C_1, C_2, C_3, A_1, A_2, A_3, q_1 and q_2 are explained in the text.

Site	Variable	Model	R^2	C_0	C_1	proportion structured variance	A_1 (m)	C_2	A_2 (m)	C_3	A_3 (m)	q_1 (m)	q_2 (m)
A	beads before rain	sill	0.52	1.07	6.50	0.86	0.64	-	-	-	-	-	-
	beads after rain	linear	0.56	0.37	-	-	-	-	-	-	-	-	-
	altitude	sill	0.99	0.00	45.12	1.00	2.89	-	-	-	-	-	-
	(altitude	gauss	0.98	0.56	15.00	0.99	0.50	19.20	0.52	10.00	0.15	1.20	2.40)
	biomass	gauss	0.84	0.00	0.10	1.00	0.43	0.07	0.22	0.05	0.10	1.60	2.80
	soil moisture	gauss	0.95	0.46	1.34	0.84	0.59	0.66	0.20	0.41	0.12	1.60	2.60
	soil temperature	gauss	0.98	0.00	1.45	1.00	0.49	1.39	0.27	1.01	0.23	1.60	2.60
	soil organic matter	spher	0.39	0.03	0.08	0.73	0.72	-	-	-	-	-	-
	NH_4-N	sill	0.46	0.14	0.37	0.73	0.70	-	-	-	-	-	-
	NO_3-N	linear	0.57	1.48	-	-	-	-	-	-	-	-	-
	PO_4-P	linear	0.90	0.00	-	-	-	-	-	-	-	-	-
	penetrability	sill	0.59	$2.84.10^{-4}$	$12.15.10^{-4}$	0.81	1.62	-	-	-	-	-	-
	texture	sill	0.82	0.00	25.15	1.00	1.31	-	-	-	-	-	-
B	beads before rain	sill	0.31	0.68	5.64	0.89	0.49	-	-	-	-	-	-
	beads after rain	spher	0.13	0.00	0.11	1.00	0.56	-	-	-	-	-	-
	altitude	sill	0.83	0.00	41.39	1.00	1.60	-	-	-	-	-	-
	biomass	sill	0.78	0.00	0.38	1.00	0.99	-	-	-	-	-	-
	soil moisture	sill	0.64	0.31	1.57	0.84	0.81	-	-	-	-	-	-
	soil temperature	sill	0.79	0.00	8.98	1.00	1.02	-	-	-	-	-	-
	soil organic matter	sill	0.80	0.03	0.07	0.70	1.34	-	-	-	-	-	-
	NH_4-N	sill	0.42	0.29	0.30	0.51	0.89	-	-	-	-	-	-
	NO_3-N	linear	0.33	31.34	-	-	-	-	-	-	-	-	-
	PO_4-P	sill	0.48	$2.08.10^{-3}$	$3.06.10^{-3}$	0.60	1.62	-	-	-	-	-	-
	penetrability	spher	0.57	$6.31.10^{-4}$	$17.88.10^{-4}$	0.74	1.62	-	-	-	-	-	-
	texture	linear	0.60	13.97	-	-	-	-	-	-	-	-	-

Site	Variable	Model	R^2	C_0	C_1	proportion structured variance	A_1 (m)	C_2	A_2 (m)	C_3	A_3 (m)	q_1 (m)	q_2 (m)
C	beads before rain	spher	0.35	1.57	2.46	0.61	1.94	-	-	-	-	-	-
	beads after rain	spher	0.23	2.41	1.92	0.44	2.00	-	-	-	-	-	-
	altitude	linear	0.87	58.27	-	-	-	-	-	-	-	-	-
	biomass	sill	0.58	0.00	27.88	1.00	0.56	-	-	-	-	-	-
	soil moisture	linear	0.69	5.07	-	-	-	-	-	-	-	-	-
	soil temperature	sill	0.56	0.00	5.18	1.00	0.49	-	-	-	-	-	-
	soil organic matter	sill	0.77	0.07	0.31	0.82	1.29	-	-	-	-	-	-
	NH_4-N	linear	0.69	2.61	-	-	-	-	-	-	-	-	-
	NO_3-N	sill	0.33	0.69	2.70	0.80	0.46	-	-	-	-	-	-
	PO_4-P	linear	0.64	$8.22.10^{-4}$	-	-	-	-	-	-	-	-	-
	penetrability	sill	0.64	$1.08.10^{-4}$	$5.16.10^{-4}$	0.83	1.43	-	-	-	-	-	-
	texture	sill	0.63	10.57	29.60	0.74	1.14	-	-	-	-	-	-

If significant linear trend surfaces ($p<0.01$) were present in the variables evaluated (see Table 4), the given variables were represented by the deviations from the trend surface before calculation of the semivariograms.

Cross-correlograms

Biomass showed a significant positive correlation with soil moisture at a lag interval of 0-0.5 m for site A and B, but for site C no significant cross-correlations occurred (Fig. 6a), meaning that biomass and moisture patterns were overlapping for site A and B, but not for site C. A significant positive cross-correlation at a lag interval of 0-0.2 m could be detected for sites A and B between beads counted after rainfall on the one hand, and biomass and soil moisture on the other hand (Figs 6b, c), which could not be attributed to microrelief (Fig. 6d). This means that run-off was less on locations close to or in vegetated patches in site A and B (but not in site C) resulting in higher soil moisture. The cross-correlograms soil organic matter - biomass showed an increasing similarity between spatial patterns going from site A to site B and from site B to site C (Fig. 6e). The range across which significant spatial dependence occurred was relatively high (0-0.7 m) for site B as compared to the other sites. Cross-correlations of NH_4-N with biomass showed that higher amounts of NH_4-N were associated with higher biomass for site C, due to the presence of perennial grass tufts, but not for site A and B (Fig. 6f).

We further found very high negative correlations between soil temperature and biomass for all sites, indicating similar but opposite spatial patterns. For site A and B lower soil temperatures were related with annual grass patches, for plot C lower soil temperatures were mainly found under perennial grass tufts (Table 4). Cross-correlations of soil temperature with soil moisture further indicated that these lower soil temperatures were correlated with higher soil moisture at locations with a relatively high biomass for site A and B, but not for site C.

Discussion

We found a nested structure of vegetation patchiness consisting of four distinct levels (Fig. 2) along the gradient of herbivore impact of transect 1 (Fig. 1). We argue that the following characteristic spatial sequence (Fig. 1) led to this nested structure. A spatially homogeneous part of the transect largely consisting of bare soil occurred close to the watering point at a distance of approximately 0-50 m. Vegetated patches of co-occurring annuals and perennials with a scale of about 7.50 m (Table 1), alternating with bare soil, existed at a distance of approximately 50-130 m from the watering point. A continuous vegetation cover was present at a distance of approximately 130-180 m and further away from the watering point. Such characteristic spatial sequence and nested structure of vegetation patchiness was not found for transect 2, for which no significant gradient of herbivore impact was present. From this follows that the nested structure as well as the characteristic spatial sequence may be attributed to the occurrence of a gradient of herbivore impact. We acknowledge, however, that we did not provide evidence for this, due to lack of replications of transects with and without an underlying gradient of herbivore impact. But still, on first inspection, our results are in line with our initial hypothesis that vegetated patches alternating with patches of bare soil would occur at intermediate herbivore impact.

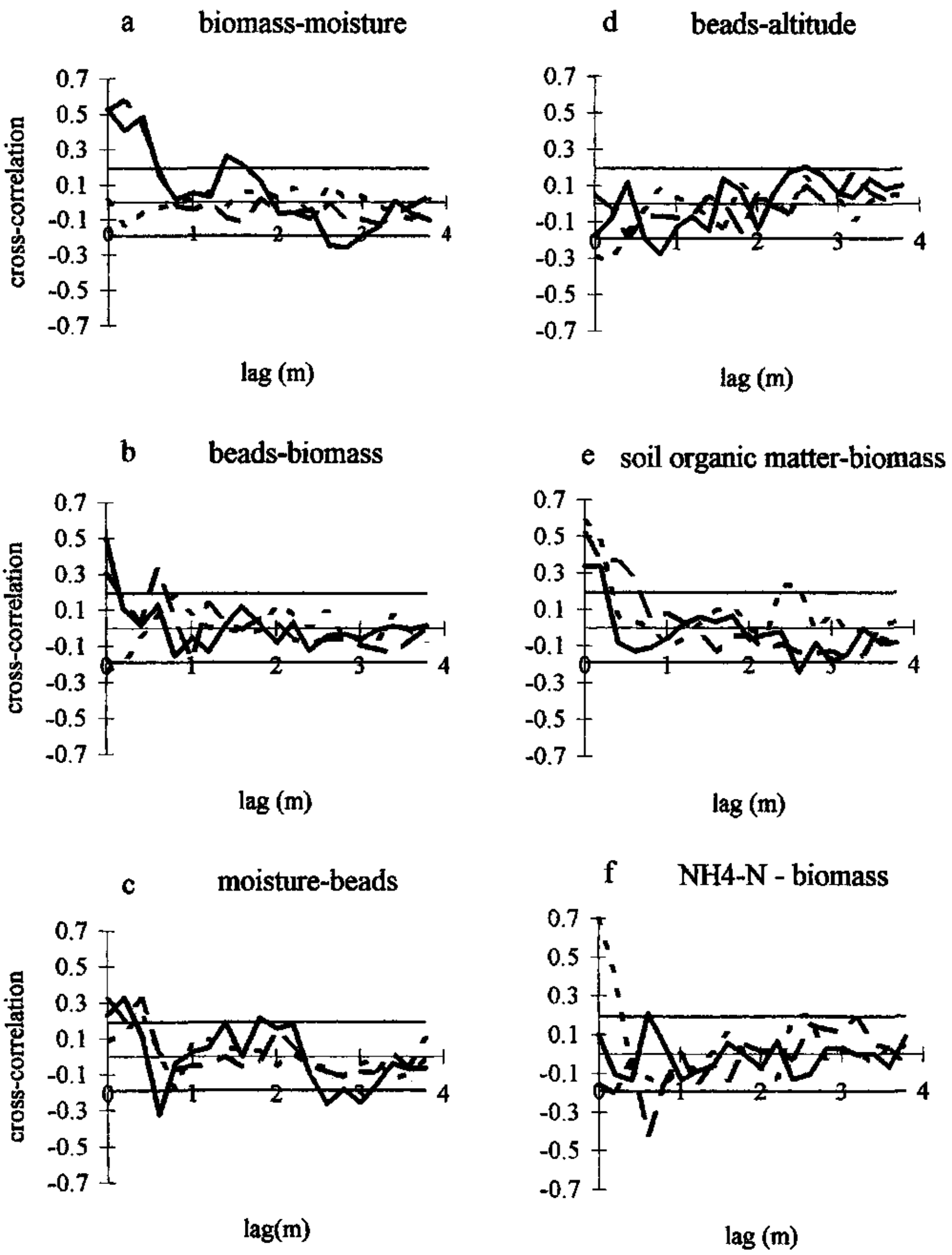

Fig. 6. Cross-correlograms of (a) biomass - moisture, (b) beads - biomass, (c) moisture - beads, (d) beads - altitude, (e) soil organic matter - biomass and (f) NH$_4$-N - biomass for site A [——], B [– – – –] and C [- - - -]. Confidence bounds indicate critical values of the correlation coefficient *r* for α =0.05 and n=105, which is the number of pairs evaluated at lag distance=0.

When analysing the data from the experimental sites along the gradient, however, we were surprised by the unexpected high degree of patchiness of vegetation and soil variables in case of low and high herbivore impact as well. In case of high (site A), intermediate (site B) and low (site C) herbivore impact, most variation of vegetation and soil variables was spatially explained, up to 100% for vegetation biomass and soil temperature (Table 5). But for low herbivore impact (site C) this was clearly due to the presence of perennial grass tufts. For high (site A) and intermediate (site B) herbivore impact, we found evidence that vegetated patches postitively affected soil moisture through less run-off and higher infiltration of rainwater that could not infiltrate into the bare soil elsewhere (Fig. 6 and Table 4). Thus, the vegetation could benefit from higher soil moisture if the soil is already vegetated. Additionally, the other side of the same coin is that vegetation could have difficulties in colonizing bare areas and becoming established due to lower soil moisture. Therefore, we conclude that in these cases a spatial pattern of vegetated patches alternating with bare soil could persist in time due to positive (self-reinforcing) plant-soil feedbacks.

The functional plant groups affected local soil properties differently. We found that perennial grass cover has a much stronger effect on infiltration capacity than annual grass cover (Fig. 3). Apparently, perennial grass tufts improve water infiltration much more effectively than annual grasses by funneling rain water via their basis into their own rhizospheres (Kelly and Walker 1976), stimulating biological activity, decreasing bulk density, thereby increasing plant available soil water (Table 2). This clearly shows the possibility for positive plant-soil feedbacks under the conditions investigated and the potential for plant-induced soil changes to persist. Our data suggest that this is especially the case for perennials. It is well known that plant-induced soil changes are more pronounced for perennials than for annuals in semi-arid grasslands, although often attention is focussed primarily on nutrient cycling (Bolton et al. 1993, Vinton and Burke 1995, but see Tongway and Ludwig 1994, for the description of a larger set of resource regulation mechanisms including water cycling). For annuals it still remains unclear at this point whether soil variability in the plots investigated is caused by specific factors such as microrelief or differential distribution of soil parent material, or by the accumulated *in situ* effects of these plants, as pointed out by the differences in soil texture between the bare soil and annual grass plots (Table 2).

The soil parent material was the same for the experimental sites along the gradient (Mulders 1996). Despite that, it seemed that differential distribution of the soil material, probably due to differences in mesorelief on site-scale, led to differences in texture between the sites (Table 3), as the present soils are sensitive to erosion (Mulders 1996). However, we propose that the differences of vegetation and the other selected soil variables between the sites A (high herbivore impact), B (intermediate herbivore impact) and C (low herbivore impact) was caused by the differences in herbivore impact and not by differential distribution of soil material. Grazing and trampling led to a relatively high coverage of bare soil, soil compaction and run-off. The availability of soil moisture was negatively affected by herbivore impact which can be explained by relatively high run-off and low infiltration for sites with a relatively low coverage of vegetation (Fig. 3), combined with the effect of high soil evaporation due to relatively high soil temperatures for these sites. These effects of grazing and trampling are commonly found in semi-arid grazing systems (Elwell and Stocking 1976, Kelly and Walker 1976, Valentin 1985). Further, it appeared that the availability of soil nutrients was also negatively affected by herbivore impact. (The high amount of NO_3-N for plot B was probably due to local deposition of animal urine.) Generally, these results contradict those of Tolsma et al. (1987) who found higher amounts of soil nutrients, including nitrogen and phosphorus, in the vicinity of two boreholes (0-100 m) as compared to longer distances away. These authors attribute this effect to the transport of nutrients by cattle via dung from surrounding areas centripetally towards the watering points, and the deposition of urine. Although we did find an increase in faeces density with decreasing distance from the watering point, this was not in agreement with the distribution of soil nutrients. We attribute this to the effects of nutrient loss through soil erosion by run-off as a consequence of the relative high coverage of bare soil and to the relative low soil organic matter related to this; effects which were not apparent in the study of Tolsma et al. (1987).

It was expected that intense grazing and trampling would have caused a relatively homogeneous bare soil. Our data, however, showed that site A (high herbivore impact) was not homogeneous at all (Table 3). The degree of patchiness was high for several variables important for explaining the total variation within this site, such as biomass, soil moisture, and soil temperature (Table 4), up to proportions of structured variance of 1.00, while for each of these variables different scales of patchiness could be determined (Fig. 5 and Table 5). These spatial patterns appeared to be mutually overlapping (Fig. 6). Further, patterns of beads after rainfall were positively correlated with biomass and soil moisture, but could not directly be attributed to microrelief (Fig. 6). We consider this as evidence of a positive effect of the occurrence of vegetation, in this case consisting of annual grasses and herbs, on soil moisture, through run-on of rainwater which could elsewhere not infiltrate into the soil (Fig. 3). At the same time, however, it appeared that the occurrence of relatively high amounts of biomass was related with microdepressions ($r=-0.3$, $p<0.05$). This, and the corresponding patchy structure of biomass, soil moisture and temperature with altitude (Fig. 5 and Table 5), leads us to the conclusion that we could not exclude microrelief as an important factor contributing to vegetation and soil patterning within this site.

For site B (intermediate herbivore impact) it was expected that the degree and scale of patchiness would be relatively high, as patches of bare soil could cause run-off of water and erodable material. Resources could subsequently become available for vegetated patches because of run-on. Indeed, as for site A, we found evidence that patches of annual grasses and herbs positively affected soil moisture through run-on of water that could not infiltrate elsewhere, while these vegetated patches had a significantly higher organic matter content (Fig. 6). Here, we could even exclude microrelief as an important factor contributing to vegetation and soil patterning, as these patterns were not overlapping. Site B was generally more homogeneous than site A when considering coefficients of variance (Table 3). However, it appeared that for variables important for explaining total variation within this site, such as biomass, soil moisture, soil temperature and soil organic matter (Table 4), sample variance as well as the proportions of structured variance were more or less comparable with site A (Fig. 5 and Table 5). Only one clear scale of patchiness of these variables could be determined (about 1.00 m).

For site C (low herbivore impact) we expected that the degree of patchiness would be relatively low, and that scales of patchiness could be attributed to the differences in the *in situ* effects that the functional plant groups have on soil resources and physical properties. Indeed, the presence of perennial grass tufts determined the scale and degree of patchiness of biomass and to a certain extent also those of soil temperature, soil organic matter and NH_4-N (Figs 5, 6 and Table 5). These variables were important for explaining total variation within this site (Table 4) and coefficients of variation and sample variance were relatively high (Tables 3, 5 and Fig. 5). The degree of patchiness was higher than we expected, up to a proportion of structural variance of 1.00 for biomass and soil temperature (Table 5). Further, redistribution of water after rain leading to higher soil moisture if vegetation in present could not be detected (Figs 4, 6).

Jackson and Caldwell (1993) and Ryel et al. (1996) found a spatial structure for NH_4-N and NO_3-N in a perennial sagebrush-wheatgrass steppe with typically a range of about 1 m and a proportion of structural variance of about 0.50, similar to our results. However, clear relationships between the location of perennial grass tufts and total soil nitrogen were not found by the above mentioned authors, while we found a clearly overlapping pattern of vegetation biomass, soil organic matter and NH_4-N due to the presence of perennial grass tufts of *Cymbopogon schoenanthus*. This was not the case for NO_3-N. The lack of significant cross-correlations between NO_3-N on the one hand and NH_4-N, vegetation biomass and soil organic matter on the other hand suggests no straightforward connection between the different, highly dynamic soil nitrogen pools (Stark 1994, Ryel et al. 1996). As instantaneous measurements of NH_4-N and NO_3-N reflect both nitrogen production and consumption, further conclusions could not be drawn about mineralization or nitrification rates (Wedin and Tilman 1990).

Ryel et al. (1996) and Schlesinger et al. (1996) speculate that spatial patterns develop most rapidly for resources which are typically most limiting to plant growth. We found that soil water is important for explaining total variation if soil water is deficient. This was mainly the case for high and intermediate herbivore impact. Under these conditions, soil water also showed a clear patchy structure, overlapping with patterns of vegetation biomass. For low herbivore impact, soil water was higher and probably not limiting. Here, no patchy structure for this variable or overlapping patterns with vegetation biomass were found. Under these conditions, soil organic matter and NH_4-N took over as important variables for explaining total variation while spatial patterns of these variables were highly overlapping with vegetation biomass. In conclusion, although based on a snapshot in time, we think that our results support the hypothesis of Ryel et al. (1996) and Schlesinger et al. (1996).

By comparing the spatial distribution of soil nutrients in desert grasslands and shrublands, Schlesinger et al. (1996) argued that changes in the distribution of soil properties may be a useful index of overgrazing in semi-arid grasslands. Their line of reasoning is that as grazing and trampling creates spatial soil heterogeneity, this may lead to the invasion of grassland communities by desert shrubs, and these shrubs further localize soil fertility leading to even more soil heterogeneity. Our data indicated that the occurrence of perennial grass tufts led to high plant-induced soil heterogeneity in case of relatively low grazing and trampling. Thus, depending on local conditions and the change in relative abundance of different functional plant groups, grazing and trampling could either lead to increased or decreased soil heterogeneity. Evidently, the fact that different functional plant groups (shrubs vs. perennial grass tufts vs. annual grasses) induce different soil changes and spatial patterning interacts with the effects of grazing and trampling. Therefore, analysis of spatial patterns in relation with grazing and trampling should be linked with the proper cause-effect relations which account for these patterns.

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Chapter 7

Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems

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Abstract

It has long been recognized that alternate vegetation states may occur in terrestrial grazing systems. This phenomenon may be of great importance because small environmental fluctuations may lead to relatively sudden and irreversible jumps between vegetation states. Early theoretical studies emphasized saturation of herbivore feeding to explain multiple stable states and catastrophic behaviour. Recent studies on semi-arid grasslands and arctic salt marshes, however, relate catastrophic events in these systems to plant-soil interactions.

Introduction

Many terrestrial grazing systems have proved to be vulnerable to changes in grazing pressure. Increase in human population size coincided with an increased grazing pressure by livestock in the Sahel region in Africa (Le Houérou 1989). Livestock numbers, including cattle, sheep and goats, have increased from 40 million in 1950 to over 125 million in 1993. Resulting vegetation changes have been dramatic. The perennial grasses that were relatively abundant in the Sahel region were replaced by annual vegetation, which is very sensitive to disturbance (Breman et al. 1980). In years with relatively low rainfall, this led to a collapse of the herbaceous vegetation (Sinclair and Fryxell 1985, Schlesinger et al. 1990) leaving a vegetation consisting of a sparse cover of unpalatable annual herbs and unpalatable shrubs (Walker et al. 1981). Eventually, these processes resulted in desertification and famine in various parts of the Sahel region (Sinclair and Fryxell 1985, Graetz 1991).

A collapse of the vegetation following changes in grazing pressure has also been reported for arctic plant communities along the coast of the Hudson Bay in Canada (Jefferies 1988a, Jefferies 1988b). The mid-continent population of lesser snow goose (*Chen caerulescens caerulescens*) has increased from 1.2 million to almost two million birds between 1973 and 1989. This has resulted in a dramatic increase in the numbers of geese that breed on the salt marshes of the Hudson Bay coast. Increase in foraging and grubbing for roots and rhizomes in the soil has led to the destruction of existing plant communities and has created large bare patches lacking organic soil.

A number of ecological indicators point to the existence of multiple stable states in the systems described above (Rietkerk et al. 1996, Chapter 2 in this thesis). First, increases in herbivore grazing pressure resulted in irreversible shifts between vegetation states in both the Sahel and along the Hudson Bay (Jefferies 1988b, Le Houérou 1989). Attempts in the Sahel to restore the former vegetation in bare areas by reducing herbivore numbers had little effect; the areas have remained in their new barren state for at least 20 years and have not reverted to their original vegetated state (Walker et al. 1981, Sinclair and Fryxell 1985, Le Houérou 1989). Secondly, mosaics consisting of densely vegetated patches alternating with almost bare areas, may also reflect multiple stable states (Wilson and Agnew 1992). These two-phase mosaics occur on different scales in semi-arid systems (Belsky 1986, Montana 1992, Ludwig and Tongway 1995a). Two-phase mosaics are also found along the Hudson Bay, most likely resulting from intensive grazing and grubbing by lesser snow geese (Srivastava and Jefferies 1995a).

Similar phenomena have been described for other grazing systems around the world. Destruction of vegetation and subsequent desertification have been related to increased herbivore grazing pressure in other semi-arid regions in Africa (Kerley et al. 1995, Milton and Dean 1995), south-western USA (Hess and Holechek 1995), the Russian Federation (Zonn 1995), Australia (Ludwig and Tongway 1995a, Ludwig and Tongway 1995b) and in American salt marshes (Miller et al. 1996). Additionally, a number of studies stress that overgrazed systems in Africa, America, and Australia cannot easily be restored on a practical time scale by simply lowering the level of herbivory (Sinclair and Fryxell 1985, Friedel 1991, Laycock 1991).

The theoretical possibility of multiple stable states in terrestrial grazing systems has long been recognized (Noy-Meir 1975, Yodzis 1989). Recent empirical studies have produced valuable insights into the causes of these phenomena. They may aid in the development of a general mechanistic framework for explaining catastrophic behaviour in terrestrial grazing systems.

Mechanistic explanations

Models that describe the dynamics of grazing systems are typically based on the same general structure (Noy-Meir 1975, Yodzis 1989). The rate of change of plant standing crop P is represented by the differential equation:

$$\frac{dP}{dt} = G(P) - C(P) \tag{1}$$

in which $G(P)$ describes plant growth as a function of plant standing crop and $C(P)$ is the loss rate due to consumption by herbivores. For example, $G(P)$ may be given by the logistic growth equation, $G(P) = r\,P\,(1 - P/K)$, whereas losses due to overgrazing are proportional to both plant standing crop and herbivore density: $C(P) = \alpha\, H\, P$ (see Boxes 1 and 2). The models often incorporate H as a fixed parameter, that is, herbivore density is assumed to be more or less constant and independent of plant standing crop. This is not unreasonable for many managed grazing systems (Noy-Meir 1975), but not necessarily applicable to more natural systems. In the example above, a single stable state is found independent of herbivore density (Fig. 1a). At low plant standing crop, plant growth exceeds grazer-induced losses. Beyond a certain plant standing crop (denoted by P_1), growth is lower than grazer-induced losses, because plant growth is limited by high vegetation density. Figure 1b shows that equilibrium plant standing crop P_1 is negatively related to herbivore density. At high herbivore density, plants cannot compensate for herbivore induced losses, and consequently plants are unable to persist in the system.

This article reviews a number of mechanisms that produce multiple stable states in terrestrial grazing systems. Two groups of mechanisms are considered: mechanisms affecting the consumption term $C(P)$ and mechanisms affecting the growth term $G(P)$ (Clark 1990).

Herbivore saturation

It is generally accepted that the rate of grazing is positively related to plant standing crop, eventually saturating at high plant standing crop (Holling 1959, Short 1985, Spalinger and Hobbs 1992). Early studies on multiple stable states in grazing systems related discontinuous dynamical behaviour to herbivore saturation (Noy-Meir 1975). Herbivores are supposed to be relatively efficient in consuming plant biomass at low plant standing crop. As a consequence, plant losses

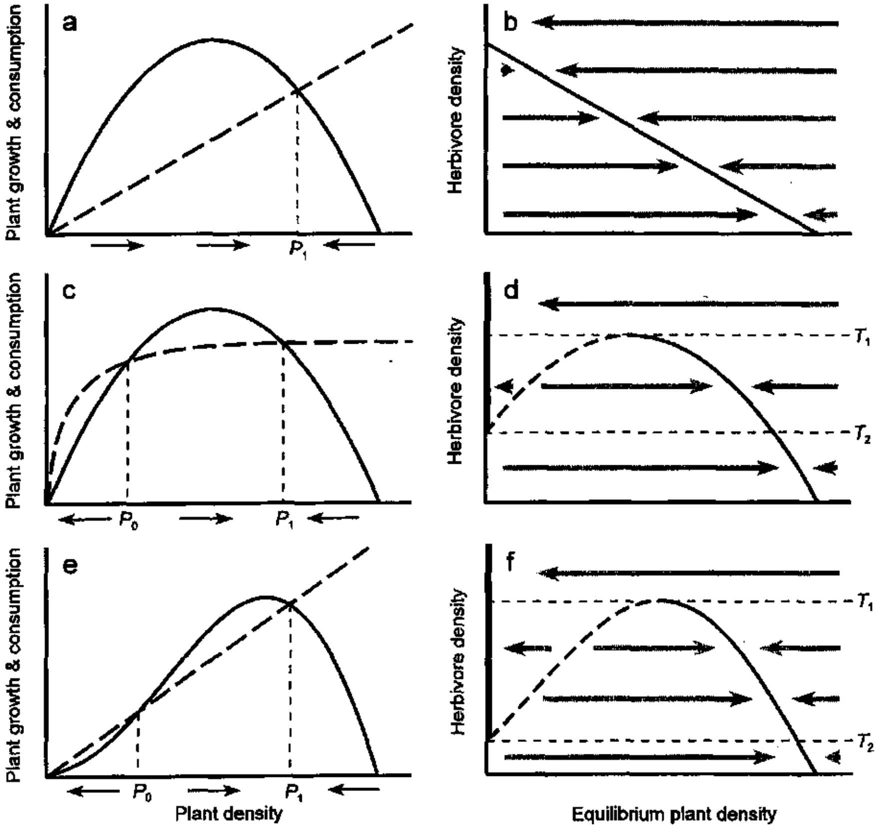


Fig. 1. (a), (c),(e) Plant growth (solid line) and plant losses (dashed line) as a function of plant standing crop. In (a) and (c), plant growth is given by the logistic equation, whereas plant growth is depressed at low plant standing crop in (e). In all cases, the losses due to grazing are assumed to be proportional to herbivore density H. In (a) and (e), losses are proportional to plant standing crop, whereas they level off at high plant standing crop in (c) due to herbivore saturation. The intersects between both curves mark the equilibria. An increase of herbivore numbers results in a proportional increase in grazing pressure, and consequently plant loss curves become steeper, whereas they level off at higher values in (c). (b), (d), (f) Relation between equilibrium plant standing crop and herbivore density. (b) Only one equilibrium occurs. (d,f) For herbivore densities below T_1 or above T_2, there is a single stable equilibrium. For any herbivore density in between T_1 and T_2, two alternate stable equilibria occur. At the threshold values T_1 and T_2, discontinuous vegetation shifts may occur if herbivore numbers are increased or decreased respectively.

exceed plant growth at low plant standing crop, which leads to further decline in plant standing crop when the system is sparsely vegetated (Fig. 1c). At intermediate plant standing crop, however, saturation of herbivore intake implies that plant growth exceeds herbivore-induced losses once plant standing crop exceeds a threshold level P_0. This results in a net increase in plant standing crop, until the upper equilibrium P_1 is reached. Beyond this upper equilibrium, net plant growth is negative due to limitations imposed by high vegetation density. Note that the steepness and convexity of the consumption curve are critical features influencing the existence of multiple stable states.

Fig. 1d shows again how equilibrium plant standing crop is affected by herbivore density. At low herbivore density, only one stable equilibrium occurs. At intermediate herbivore densities, the model predicts that there are two stable states. One state is vegetated, whereas the other is barren due to overgrazing. At high herbivore densities, only the overgrazed state is possible. Hence, the vegetation inevitably collapses to the bare state when herbivore density is higher than the threshold level T_1. A sustainable vegetation state is not restored when herbivore density is diminished, unless density is reduced below a second threshold T_2.

Following Noy-Meir (1975), a number of studies have stressed the importance of herbivore saturation for the existence of stable states and threshold effects. However, multiple stable states can also occur in the absence of herbivore saturation, that is, at a plant standing crop were herbivore saturation does not yet play a role. Various mechanisms, most notably soil degradation, depress plant growth at low plant standing crop (see Fig. 1e). As a result, the growth and consumption curves may intersect twice, even in the absence of herbivore saturation.

Soil degradation

A large body of literature exists relating vegetation shifts in semi-arid grasslands to soil degradation (Elwell and Stocking 1976, Kelly and Walker 1976, Breman and De Wit 1983, Sinclair and Fryxell 1985, Le Houérou 1989). Vegetation improves the structure and water-holding capacity of the soil, preventing crust formation through the interception of raindrops. Vegetation protects the soil against erosion by physical binding of soil, and the retention of surface water. Soil degradation occurs if plant standing crop is insufficient to prevent surface run-off of rain water. As a consequence, the proportion of the rainfall that infiltrates into the soil decreases (Kelly and Walker 1976). Furthermore, run-off of water often leads to loss of nutrients via soil erosion (Kiepe 1995). Elwell and Stocking (1976) showed that both run-off and soil erosion increase when vegetation cover decreases (see Fig. 2). In systems in which water or nutrients are limiting plant growth, as in most semi-arid regions, we may expect plant growth to decline when run-off and loss of nutrients occur. This may trigger a positive feedback between reduced plant standing crop, reduced water and nutrient availability, and reduced plant growth.

Walker et al. (1981) modelled competition between woody vegetation and grasses for available soil water. Their model includes reduced water infiltration into the soil when the cover of grasses is low, as well as a saturating herbivore functional response. Two stable states emerge in their analysis: one state with both grasses and woody vegetation, and one degraded state with only woody vegetation. Treating the vegetation as a single state variable, Rietkerk and Van de Koppel (1997) (Chapter 3 in this thesis) show that herbivore saturation is not essential for this conclusion since, in essence, reduced water infiltration at low plant standing crop is sufficient to explain catastrophic behaviour. They show that, in water limited systems, per capita plant growth may be reduced at low plant standing crop due to reduced water infiltration (see Box 1).

Box 1. Feedback between plant standing crop and water infiltration

Here, we present a simplified version of the water-limitation model analyzed by Rietkerk and Van de Koppel (1997) (Chapter 3 in this thesis). In semi-arid systems, plant growth is mainly limited by the availability of water (Breman and De Wit 1983). Therefore, plant growth increases if water availability increases. Assume that the dynamics of the plant population P is characterized by the following differential equation:

$$\frac{dP}{dt} = rP(1-\frac{P}{K})f(W) - \alpha HP,$$

where r is a plant growth coefficient, K is the carrying capacity of the vegetation, $f(W)$ is a function describing the effect of water availability W on plant growth, α is a herbivore consumption coefficient, and H is herbivore density. For example, $f(W)$ might be given by $f(W) = W/(W+b)$, where b determines how quickly growth increases with water availability.

The availability of soil water is governed by a number of factors, including water infiltration, losses of water from the soil due to evaporation and percolation, and the uptake of water by plants. The changes in water availability due to these factors may be represented by a differential equation:

$$\frac{dW}{dt} = W_{in}\frac{P+aq}{P+a} - eW - uWP.$$

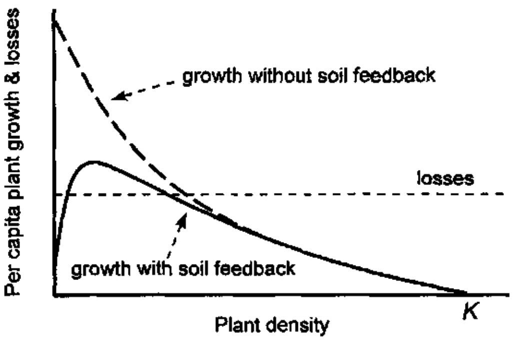
Here, water infiltration is an increasing but saturating function of plant standing crop P. W_{in} stands for rainfall, a determines how quickly infiltration increases with plant standing crop, q is the fraction of rainfall that infiltrates into bare soils, e is the specific loss rate of water from the soil and u is a plant uptake coefficient. Since the dynamics of soil water act on a much faster time scale than growth of plants, we assume soil water conditions to be in equilibrium with respect to plant growth [a quasi-steady-state approach (Edelstein-Keshet 1988)]. The equilibrium condition $dW/dt = 0$ yields water availability $W^*(P)$ as a function of plant standing crop. In our example, $W^*(P)$ is given by

$$W^*(P) = W_{in}\frac{P+aq}{P+a}\ \frac{1}{e+uP} \ .$$

Insertion of $W^*(P)$ into the function f yields the plant growth curve:

$$G(P) = rP(1-\frac{P}{K})f[W^*(P)].$$

which resembles the growth curve in Fig. 1e. Hence, multiple stable states and catastrophic changes between states are possible if water infiltration is positively related to plant standing crop. An alternative representation is given in the figure below which shows per capita growth ($G(P)/P$) and losses ($C(P)/P$) as a function of plant standing crop. The per capita rate of plant growth is reduced due to water limitation, relative to a model without soil feedback (obtained if $a = 0$).



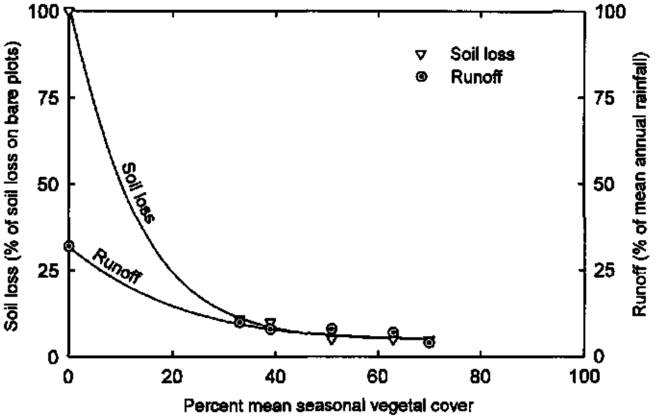


Fig. 2. Mean annual soil loss (triangles) and run-off (circles) as a function of vegetation cover. Reproduced, with permission, from Elwell and Stocking (1976).

Similarly to the Sahel region, edaphic changes appear to be a key factor in the desertification of the salt marshes of the Hudson Bay. Srivastava and Jefferies (1996) show that a positive feedback exists between plant standing crop and soil salinity, such that decreased plant standing crop increases soil salinity, which in turn decreases plant growth (Fig. 3). The decrease of plant standing crop by goose grazing results in increased soil evaporation and deposition of salts in the upper layer of the soil (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1995b). The resulting saline soils inhibit the growth and survival of plants (Srivastava and Jefferies 1995a, Srivastava and Jefferies 1995b), thereby further reducing plant standing crop, in turn resulting in more bare soil. A simple model reveals that this feedback can reduce plant growth at low plant standing crop (see Box 2).

The implications of plant-soil feedbacks on the dynamics of grazing systems are illustrated by Figs 1e, f. At low plant standing crop, soil degradation occurs, resulting in reduced per capita plant growth, as is explained in Boxes 1 and 2. As a result, total plant growth $G(P)$ is upwardly convex at low plant standing crop. The growth and loss curves may now intersect twice (Fig. 1e). Plant growth is lower than plant losses at low plant standing crop, whereas it exceeds plant losses at intermediate plant standing crop. As a result, two stable states may occur within this system, even without saturating herbivore foraging. In one state, deteriorated edaphic conditions do not allow plants to compensate for losses, and this state lacks vegetation. Edaphic conditions are suitable for plant growth in the other state, allowing plants to compensate for grazer induced losses. Therefore, vegetation persists at this equilibrium.

The model yields predictions similar to the model with herbivore saturation. The system has a single vegetated state at low herbivore density. Two stable states occur at intermediate herbivore density. One state is bare, whereas the other is vegetated. At high herbivore density, plants cannot persist. Only one stable state exists, which is devoid of vegetation. There are, once again, two threshold herbivore densities T_1 and T_2 (Fig. 1f), at which catastrophic changes are to be expected if herbivore density is changed. Hence, soil degradation models offer an alternate mechanistic explanation for catastrophic vegetation shifts in terrestrial grazing systems.

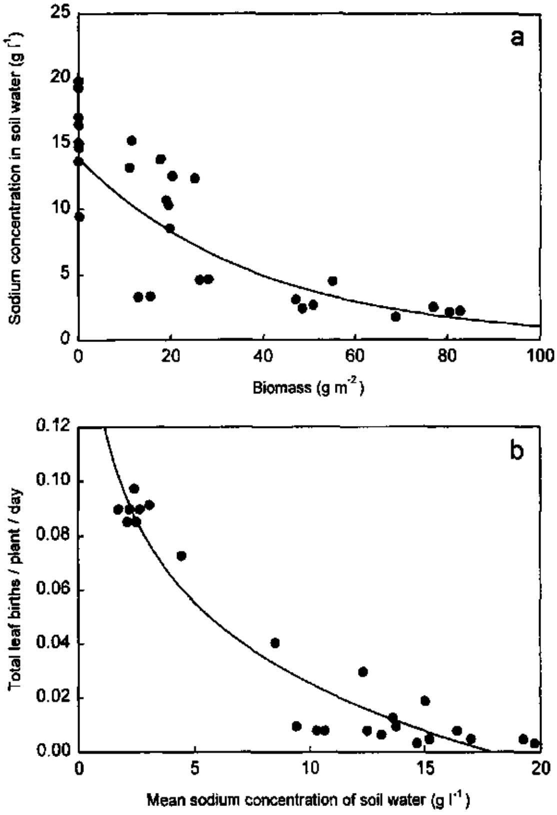


Fig. 3. Relationship between (a) sodium concentration in soil water and plant standing crop, and (b) total leaf birth rate and the sodium concentration in soil water, in an arctic coastal salt marsh. Reproduced, with permission, from Srivastava and Jefferies (1996).

Box 2. Feedback between plant standing crop and soil salt levels

A simple model for the interaction between soil salt levels and plant growth shows the potential for alternate stable states in the arctic salt-marshes along the Hudson Bay. Srivastava and Jefferies (1996) showed that per capita plant growth decreases with increasing salt levels (as is shown in Fig. 3b). Total net plant growth, therefore, might therefore be given by a differential equation of the form:

$$\frac{dP}{dt} = rP(1-\frac{P}{K})f(S) - \alpha HP,$$

where P is plant standing crop, r is the intrinsic growth rate of plants, K is the carrying capacity, $f(S)$ is a function describing the effect of the salt level S on plant growth, α is a herbivore consumption coefficient, and H is herbivore density. A simple example of a salt-limitation function is $f(S) = e^{-bS}$, where b is a scaling parameter.

Srivastava and Jefferies furthermore indicate that a negative relation exists between salt levels in the soil and plant standing crop (Fig. 3a). This relation might be described by a function $S(P) = S_{max}\, e^{-cP}$, where S_{max} is the soil salt level when the soil is bare, and c is a scaling parameter. For the sake of simplicity, we assume that the salt level in the upper soil reacts rapidly upon plant standing crop. In this case, the salt level is a function $S(P)$ which upon insertion into the function f yields the plant growth curve:

$$G(P) = rP(1-\frac{P}{K})f[S(P)].$$

This growth function yields the growth curve in Fig. 1e. Hence, multiple stable states and catastrophic vegetation changes are possible if salt levels in the soil relate negatively to plant standing crop. Similar to Box 1, the per capita rate of plant growth is reduced relative to a model without soil feedback, due to high salt levels at low plant standing crop.

A large number of soil-related processes may cause decreased per capita plant growth at low plant standing crop (Wilson and Agnew 1992). For instance, soil losses, due to wind erosion or run-off of water, may reduce nutrient availability at low plant standing crop (Jefferies 1988a, Schlesinger et al. 1990). Hence, per capita plant growth may be reduced when plant standing crop is low, especially in nutrient-limited systems (Rietkerk and Van de Koppel 1997, Chapter 3 in this thesis). The presence of dry or tough algal crusts may reduce shoot survival and leaf production, in particular on bare soils or in low density vegetation (Srivastava and Jefferies 1995b, Grootjans et al. 1997). These algal crusts are rarely found in sites with abundant vegetation. Enhanced soil evaporation or high soil temperatures may also adversely affect plant growth on bare soils (Iacobelli and Jefferies 1991, Belnap 1995, Srivastava and Jefferies 1995a). Changes in soil albedo may lead to reduced rainfall in bare regions as compared to vegetated regions (Charney et al. 1975). These processes may cause positive feedbacks between plant growth and plant standing crop, and lead to vegetation collapse, even without increased herbivory. Herbivory may, however, expose these positive feedbacks by (1) reducing plant standing crop, which may result in soil degradation and hence in reduced plant growth, and (2) increasing plant losses, which makes it more difficult for plants to cope with conditions that are deleterious for growth.

The systems described in this review have an important characteristic in common. In all cases, herbivore density increased independent of vegetation conditions. In the Sahel region, settlement of pastoral herdsmen in villages and around waterpoints caused increased grazing pressure on local vegetation, independent of within and between-year changes in plant productivity (Sinclair and Fryxell 1985). Improved medical and veterinary aid (amongst other reasons) led to rapid increase in livestock numbers. As a result, every settlement became the centre of its own desert (Wade 1974). On the arctic salt marshes, increased goose density resulted from decreased mortality on their wintering grounds and on the flyways. Despite the deterioration of vegetation, herbivore numbers remain high in both the Sahel and along the Hudson Bay. In grazing systems in which herbivore density is dependent of local plant standing crop, herbivore numbers may collapse once plant standing crop has diminished below a grazing threshold (Drent and Prins 1987). This, in turn, may prevent herbivores from severely disturbing their own food supply. Hence, these systems may be more resistant to increases in grazing pressure.

Conclusions

Two potential mechanisms for catastrophic vegetation shifts in terrestrial grazing systems are reviewed in this paper. The first is based on herbivore feeding characteristics, whereas the second is focused on plant-soil relationships. A number of empirical studies indicate that plant-soil feedbacks are the dominant cause of catastrophic behaviour in many terrestrial grazing systems. In these studies, a herbivore-induced decrease of plant standing crop has led to soil degradation and reduced plant growth. Positive feedback between reduced plant standing crop and deteriorated soil conditions has thereby contributed to irreversible vegetation destruction. It is conceivable that both mechanisms act simultaneously in many natural systems.

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Chapter 8

General discussion

Introduction

The main aim of this thesis was to provide an effective explanation of the catastrophic properties of semi-arid grazing systems. We found that soil degradation (i.e. soil erosion by run-off and wind, and the consequent loss of water and nutrients) does provide this, and this thesis brings together a number of papers on the relation between soil degradation and catastrophic vegetation dynamics in these grazing systems. In this chapter I firstly want to stress the most important results from and the coherence between the different preceding chapters. I then discuss the applicability of our models to other grazing systems. We omitted the complicating interactions between functional plant groups in our mathematical models and field experiments, and we excluded the effects of herbivore functional responses and herbivore regulation. Therefore, the effects of these factors on the dynamics of semi-arid grazing systems are also discussed, and I highlight topics for future research. Furthermore, I discuss the practical relevance of this thesis in the light of the development and implementation of pastoral management strategies.

Catastrophic vegetation dynamics and soil degradation

After translation into the state-and-transition formulation, the Sahelian example of vegetation dynamics can be interpreted in terms of catastrophe theory resulting in the detection of five catastrophic properties: bimodality, inaccessibility, sudden jumps, divergence and hysteresis (Chapter 2). In general, a legitimate criticism against the *post hoc* interpretation of observed dynamics in terms of catastrophe theory is that it fails to explain the underlying mechanisms of catastrophic behaviour (May 1977, Saunders 1980). Despite this, our application of catastrophe theory appeared to be a very useful first step in the growth of our ideas. It translated rather vague concepts into a verifiable format by deducing hypotheses about the conditions under which catastrophic vegetation dynamics may be expected. But perhaps the most valuable contribution of this exercise was that it generated the notion that soil degradation could somehow be an important factor attributing to catastrophic vegetation dynamics. We used the minimal modelling approach to investigate if soil degradation can indeed explain catastrophic behaviour mechanistically (Chapter 3). Or, worded differently, we tested the hypothesis that soil degradation may cause catastrophic vegetation dynamics by performing a thought experiment.

Our model studies indeed show that soil degradation can effectively explain the catastrophic properties of semi-arid grazing systems. Self-reinforcing plant-soil feedbacks between water infiltration or nutrient retention and vegetation biomass may lead to decreasing soil water or nutrient levels with decreasing biomass, followed by a reduction of biomass production. This positive feedback loop can be triggered by grazing. We propose on the basis of a large body of emperical literature that this is an important mechanism causing catastrophic vegetation dynamics in semi-arid grazing systems (Chapter 3). Furthermore, our model studies predict for which site-specific properties catastrophic vegetation dynamics may be expected, that is on loamy or clayey soils in case of water-limited vegetation biomass production, and on sandy soils in case of nutrient-limited biomass production. This is because sandy soils have higher infiltration rates than loamy or clayey soils, and sandy soils are more vulnerable to nutrient loss through erosion than loamy or clayey soils (Chapter 4).

An important implication of positive plant-soil feedbacks for ecosystem function also lies in the potential for plant-induced soil changes to persist and for yielding relatively heigh levels of primary productivity (Wedin and Tilman 1990, Van Breemen 1993). Thus, positive plant-soil feedbacks between water infiltration or nutrient retention and vegetation biomass may also lead to increasing soil water or nutrient levels with increasing biomass, followed by an increase of biomass production leading to even higher soil water and nutrient availability. This is only possible, however, if initial biomass and resource levels are carried above certain breakpoint values (Chapters 3, 4).

In a semi-arid savanna, we investigated the effects of aboveground biomass removal, including litter and perennial grass tufts, on soil water content and subsequent effects on tuft production (Chapter 5). Based on our models, we hypothesized that the removal of biomass would lead to a reduced soil water content and tuft production because of reduced water infiltration and increased run-off. Indeed, as a consequence of biomass removal, a reduction in soil water content and tuft production occurred. But, it appeared that the increased loss of soil water through increased soil evaporation as a consequence of litter removal ultimately outbalanced all other effects on soil water content. Several factors might have contributed to the importance of increased soil evaporation, overriding that of reduced water infiltration and increased run-off. The soil in the research area was a sandy loam, with higher infiltation rates than soils with a lower percentage sand and higher percentage clay, while rainfall primarily occurred in light showers. Thus, under these conditions, when the plant-soil feedback between reduced water infiltration and reduced biomass does not operate (Chapter 4), another plant-soil feedback that is between increased soil evaporation and reduced biomass may become prominent.

The occurrence of vegetation mosaics, consisting of densely vegetated patches alternating with almost bare soil, may be an ecological indicator of catastrophic vegetation dynamics. Therefore, we studied vegetation patchiness along a gradient of herbivore impact, consisting of a radial pattern of "high", "intermediate" and "low" herbivore impact around a watering point in a semi-arid grazing system (Chapter 6). At low herbivore impact, vegetation patchiness could be attributed to the occurrence of perennial grass tufts. At high and intermediate herbivore impact, vegetated patches positively affected soil water through less run-off and higher infiltration of rainwater that could not infiltrate into the bare clay loam soil elsewhere. But at high herbivore impact microrelief could not be excluded as an important factor contributing to vegetation patchiness. Thus, the occurrence and likely persistence of a spatial pattern of vegetated patches alternating with bare soil at intermediate herbivore impact could be explained by the positive plant-soil feedback between vegetation biomass and water infiltration. This observed pattern is in line with our models (Chapters 3, 4), but it illustrates a marked difference at the same time. In our models, soil water and nutrients that can not be retained and used by the vegetation are completely lost from the system. However, we provided evidence that in reality these resources are potentially available for vegetation elsewhere. This cries out for the incorporation of spatial explicit processes in the models as this may accurately predict the formation and persistence of vegetation and soil patches under different conditions. These predictions can subsequently be used as hypotheses that can be tested in the field. I expect that this approach may lead to a more thorough understanding of the implications of plant-soil feedbacks for the dynamics of semi-arid grazing systems, including their so characteristic spatial and temporal heterogeneity. Therefore, this should be a priority on the research agenda for the coming years.

General applicability

Our models focus on simple cases by omitting many complicating ecological factors that may occur in reality. Our point that plant-soil feedbacks can cause catastrophic vegetation dynamics triggered by grazing can therefore be even further generalized (Chapter 3). Any positive plant-soil feedback that is strong enough may cause catastrophic vegetation dynamics, which, consequently, can be triggered by any factor influencing vegetation production. Thus, our models of positive feedback loops leading to catastrophic dynamics may also apply to other ecosystems. In their study of an arctic salt marsh, Srivastava and Jefferies (1996) showed that a plant-soil feedback exists between soil salinity and vegetation biomass. A decreased vegetation biomass increases soil salinity through increased soil evaporation. This, in turn, decreases biomass production, leading to an even more saline soil. Increased grazing by lesser snow geese (*Chen caerulescens caerulescens*) triggered the positive feedback loop, with desertification as a result. In intertidal mudflat systems, benthic diatoms mats protect sediment against erosion by excreting polysaccharides. In case of decreased diatom density the sediment becomes highly sensitive to erosion by tidal currents (Daborn et al. 1993, Underwood and Paterson 1993). This will likely lead to increased diatom loss, resulting in a reduction of diatom production and even more erosion (Van de Koppel pers. comm.). This positive feedback loop could be triggered by increased grazing on diatoms by for example the amphipod *Corophium volutator*, especially when predation by migratory birds feeding on *Corophium* is low (Daborn et al. 1993). Several studies report about similar feedbacks that could also be related to catastrophic dynamics in a wide variety of ecosystems (reviewed by Wilson and Agnew 1992, Chapter 7). Thus, I think that our models provide insights of general importance.

Interactions between functional plant groups

One of the complicating factors that we omitted in our models and field experiments is the interaction between plant functional groups: woody vs. herbaceous plants and non-woody perennials vs. annuals. The general model for the interaction between woody and herbaceous plants in semi-arid savannas is that of a two layered soil water system, in which each functional group is the superior competitor for available soil water in a different soil layer (Walker et al. 1981). Herbaceous plants are more efficient in extracting water from the topsoil, whereas woody plants have better access to water that percolates through the topsoil and infiltrates into the subsoil (Knoop and Walker 1985, Sala et al. 1989, Brown and Archer 1990). The model of Walker et al. (1981) predicts that this may lead to the development of two alternate stable states in semi-arid savannas: one with relatively much woody vegetation, and one with relatively much herbaceous vegetation and rather little woody vegetation. The facts that herbaceous plants may also have access to the subsoil (Knoop and Walker 1985) and woody plants to the topsoil (Le Roux et al. 1995, Le Roux and Bariac 1998) do not invalidate these predictions [although Le Roux and Bariac (1998, p. 465) call it "a misleading simplification"]. At the same time, woody plants in semi-arid savannas add nutrients to the understorey environment in the shrub or tree crown zone in the form of litter and droppings of reposing animals, and reduce soil and plant temperatures and evapotranspiration by the shade they cast (Kellman 1979, Belsky et al. 1989, Belsky 1994). Hence, if the benefits of higher water and nutrient levels exceed the costs of lower light levels, woody plants also facilitate herbaceous plants.

In semi-arid grasslands where no or few woody plants occur, this interplay takes mainly place between non-woody perennials and annuals. When explaining the relative abundance of perennial and annual grasses, the discussion in the literature focusses on the differences in phenology of seed production and vegetative growth between them, in relation to the timing of major forces driving these developmental events, such as rainfall (Prins 1988, Prins and Loth 1988, Sarmiento 1992, Veenendaal et al. 1996). Once established, perennial grasses form a network of living roots and (underground) stems, through which the plants can reproduce vegetatively. It is undisputed that this gives them an important advantage over annual grasses when competing for water (Chapter 2). At the same time, both functional groups improve water availability by increasing water infiltration and decreasing soil temperatures thereby reducing soil evaporation (Chapters 5, 6). Furthermore, perennial grasses may improve nutrient availability around individual tufts (Chapter 6, Jackson and Caldwell 1993). Hence again, if the benefits of higher water and nutrient levels outbalance the costs of lower levels by competition, perennial grasses and annual grasses may also facilitate each other.

Hence, together with grazing, it is the outcome of the interplay of facilitation and competition (cf. Holmgren et al. 1997, Brooker and Callaghan 1998) within and between functional plant groups that ultimately determines the vegetation state of semi-arid grazing systems. I am not aware of any experimental studies investigating this interplay between perennial and annual grasses within the herbaceous layer of semi-arid grasslands. This is an area of research that deserves a higher priority in the near future.

Herbivore functional responses

Noy-Meir (1975) stressed that vegetation dynamics can show catastrophic properties as a consequence of the non-linear shape of the functional response of the herbivore to changes in forage availability. In this thesis we stress that a non-linear herbivore functional response is not a necessary condition, and that positive plant-soil feedbacks are sufficient and more likely to explain catastrophic vegetation dynamics. This does not mean that we invalidated the models of Noy-Meir (1975). To illustrate this I now turn to a theoretical reflection on our model assumptions regarding herbivore functional responses.

Consider the water-limitation model as described in Chapter 3 and mathematically explicitely defined in Chapter 4. Recall that herbivore consumption rate, which I call now $C(P)$, was given by

$$C(P) = bP \tag{1}$$

where b is specific plant loss due to herbivory and P is plant density. Equation 1 can be rewritten as

$$C(P) = \alpha hP \tag{2}$$

where α is a herbivore consumption coefficient and h is herbivore density. As both the herbivore consumption coefficient α and herbivore density h are independent of plant density P, the plant isocline in the phase plane is a straight, vertical line (Fig. 1a) (Chapter 3). In case of no positive plant-soil feedback between water infiltration and plant density, there is only one stable internal equilibrium at (W^*,P^*) if $W^*<W_s$, where W is soil water availability W^* is the minimal amount of soil water necessary for plants to colonize bare areas and W_s is the equilibrium amount of soil water in the absence of plants. Thus, we concluded that alternate stable states and threshold effects do not occur (Chapter 3). I will now relax the assumption of a linear functional response and investigate the effects of a saturating (Holling Type II), sigmoid (Holling Type III) and hump-shaped response (Van de Koppel et al. 1996). Throughout this exercise I will stick to the assumption that no positive plant-soil feedback between water infiltration and plant density operates.

The saturating functional response can be presented by the equation

$$C(P) = c_{\max} h \frac{P}{P+k} \tag{3}$$

where $c_{\max}$ is the maximum consumption rate of the herbivore and k is a half saturation constant. As the herbivores become saturated at high plant density, the plant isocline bends to the left (Fig. 1b). Now, if $W^*>Ws$, the system can be characterised by two stable equilibria, one boundary equilibrium at (W_s,0) and one internal equilibrium at (W_1*,P_1*). In this case, evidently, alternate stable states and threshold effects may occur because of the effect of herbivore saturation. This result is near-identical with the findings of Noy-Meir (1975).

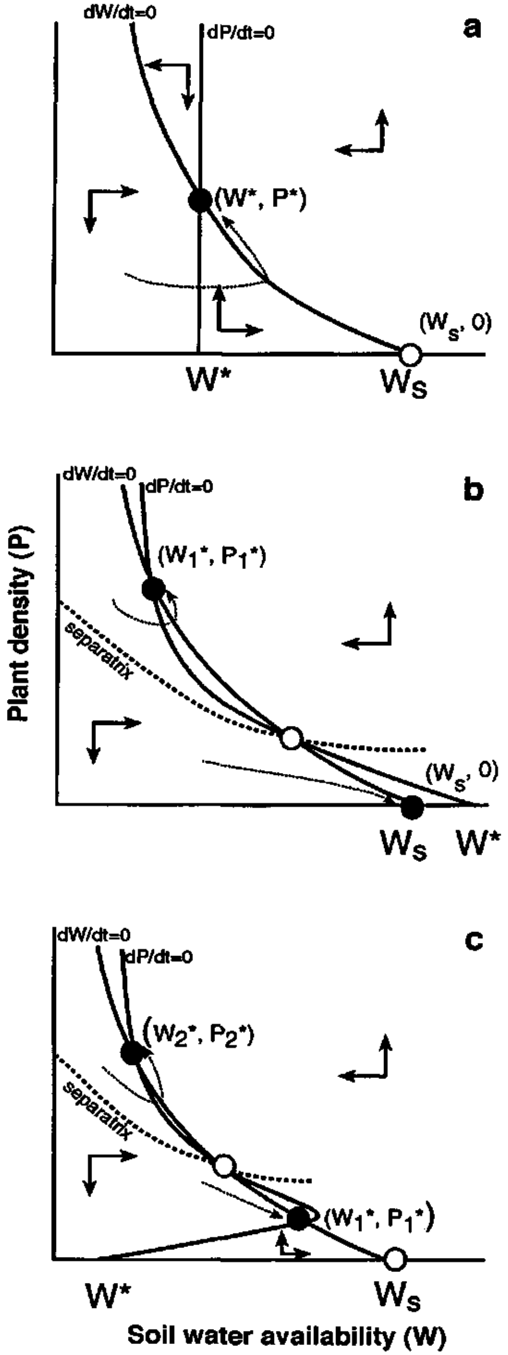

Fig. 1. (a) The zero-isoclines for plant density (dP/dt = 0) and soil water (dW/dt = 0), in case of no plant-soil feedback between water infiltration and plant density, illustrated in the phase-plane. The vectors indicate the direction of change. The dotted line illustrates the path that the system follows during time, given the starting point as indicated. W* is the minimal amount of soil water necessary for plants to colonize bare areas. W_s is the equilibrium amount of soil water in the absence of plants. The dark circle is a stable equilibrium at (W*,P*) and the light circle is an unstable equilibrium at (W_s,0). Note that W*<W_s. A linear herbivore functional response is assumed. (b) If a saturating (Holling Type II) or hump-shaped (Van de Koppel et al 1996) herbivore functional response is assumed, the system can be characterized by two stable equilibria at (W_s,0) and (W_1*,P_1*). Note that W*>W_s. (c) If a sigmoid (Holling Type III) functional response is assumed, the system can also be characterized by two stable equilibria at (W_1*,P_1*) and (W_2*,P_2*). Note that W*<W_s.

The explicit form of the sigmoid functional response is given by

$$C(P) = c_{\max} h \frac{P^2}{P^2 + k^2} \tag{4}$$

Here, herbivore consumption rate is relatively low at ranges of low plant density, for example due to the presence of an ungrazable plant reserve (Noy-Meir 1975). With increasing plant density, consumption rate increases disproportionally, until a certain point where the herbivores start to become saturated. Therefore, the plant isocline shows a hump; the hump's peak is the plant density where the herbivores start to become saturated (Fig. 1c). Now, if $W^* < Ws$, the system can be characterised by two internal equilibria, one at (W_1^*, P_1^*) and one at (W_2^*, P_2^*). Again, the same as was found by Noy-Meir (1975), alternate stable states and threshold effects may occur because of the effects of the presence of an ungrazable plant reserve and of herbivore saturation.

The hump-shaped herbivore functional resonse can be written as

$$C(P) = c_{\max} h \frac{P}{P + k} e^{(-fP)} \tag{5}$$

where $e^{(-fP)}$ is a facor reducing herbivore consumption rate with increasing forage availability, for example because dense stands are more difficult to handle (Van de Koppel et al. 1996). Incorporating this functional response in the model leads to qualitatively identical behaviour as the saturating functional response (Fig. 1b). The plant isoline shifts to the left because at high plant density a combination of herbivore saturation and handling difficulties lead to lower intake rates than when a linear functional response is considered.

Thus, herbivore saturation, handling difficulties of herbivores at dense vegetation stands, the presence of an ungrazable plant reserve and positive plant-soil feedbacks can all cause catastrophic vegetation dynamics, i.e. alternate stable states and threshold effects. It is conceivable that more than one mechanism act simultaneously in many grazing systems, and that catastrophic properties can still be detected in the absence of a positive plant-soil feedback.

Herbivore regulation

Herbivore density depends mainly on natural reproduction and mortality if it is not tightly controlled by man. This is the case in simple herbivore-plant systems, where herbivore reproduction and mortality are regulated by herbivore and plant density only. Noy-Meir (1975) showed that the stability properties of such simple herbivore-plant systems are near-identical to those of simple predator ("herbivore") - prey ("plant") systems (Rosenzweig and MacArthur 1963, Rosenzweig 1969, 1971). The non-linear herbivore functional response causes a hump in the plant isocline in herbivore-plant systems (Noy-Meir 1975). Analogously, the non-linear predator functional response causes a hump in the prey isocline in predator-prey systems (Rosenzweig

1969). Accordingly, it is interesting to examine the effect of a positive plant-soil feedback on the stability properties of a herbivore-plant model and how this corresponds to these classic herbivore-plant and predator-prey models. Therefore, I return to the situation of the linear functional response and investigate the effects of a positive plant-soil feedback between water infiltration and plant density on a dynamic herbivore population.

I originally assumed that herbivore density h is independent of plant density P. But herbivore density H is now regulated by plant density P, thus both are described by a differential equation:

$$\frac{dP}{dt} = r\left(1-\frac{P}{K}\right)Pf[W(P)] - \alpha HP \tag{6}$$

$$\frac{dH}{dt} = \beta HP - dH \tag{7}$$

where r is a plant growth coefficient, K is the carrying capacity of the vegetation, β is a herbivore growth coefficient, d is the specific herbivore mortality and $f[W(P)]$ is a function defining the plant-soil feedback (Chapter 7). In case of no plant-soil feedback $f[W(P)]=1$ and if the plant-soil feedback operates $1 > f[W(P)] > 0$, the exact value depending on soil water availability W, which, in turn, depends on plant density P. The other parameters follow the earlier defined models. In the case of no plant-soil feedback, both the plant isocline and the herbivore isocline are straight lines, resulting in a herbivore-plant system with an equilibrium (P^*,H^*) that is stable, independent of herbivore mortality d or herbivore growth coefficient β (Fig. 2a). For a detailed mathematical analysis of this model, see Edelstein-Keshet (1988).

If the plant-soil feedback operates, the form of the plant isocline is a hump, because plant growth is depressed at low plant density due to water-limitation (Fig. 2b). Now, as a consequence of the plant-soil feedback, the herbivore-plant system will ordinarily destabilize and not persist if herbivore mortality d is low or if the herbivore growth coefficient β is high and the herbivore isocline is situated at the left hand side of the hump's peak.

This model corresponds to the classic herbivore-plant models of Noy-Meir (1975). Thus, both a non-linear herbivore functional response and a positive plant-soil feedback cause a hump in the plant isocline, leading to stability properties of the herbivore-plant system that are near-identical. Given a certain herbivore density, both mechanisms cause that plant growth can not compensate for herbivore consumption at low plant density, while at higher density the reverse is true (Fig. 2b) (Chapters 3, 7).

Furthermore, this model is also equivalent to the classic predator-prey models of Rosenzweig and MacArthur (1963) and Rosenzweig (1969, 1971). The analogy can probably be best explained as follows. The positive plant-soil feedback in herbivore-plant systems can be interpreted as self-facilitation of plant production. This corresponds to the Allee (1951) effect of social facilitation of prey reproduction that causes a hump in the prey isocline in predator-prey systems (Rosenzweig 1969).

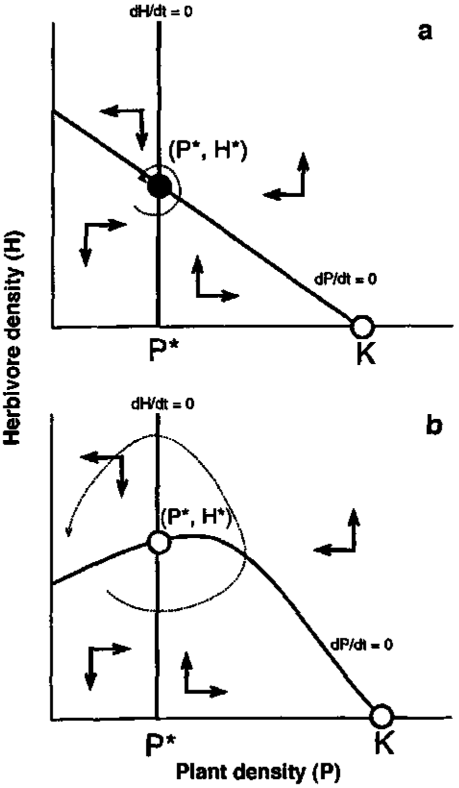

Fig. 2. (a) The zero-isoclines for herbivore density (d*H*/d*t* = 0) and plant density (d*P*/d*t* = 0), in case of no plant-soil feedback between water infiltration and plant density, illustrated in the phase plane. *P** is the minimal plant density necessary for herbivore production. *K* is the equilibrium plant density in the absence of herbivores or the carrying capacity of the vegetation. There is one stable equilibrium at (*P**,*H**), the equilibrium (*K*,0) is unstable. (b) If the plant-soil feedback operates, the form of the plant isocline is a hump. If the herbivore isocline is situated at the left hand side of the hump's peak, the equilibrium (*P**,*H**) becomes unstable and the herbivore-plant system will ordinarily not persist.

Thus, "explosive" (Rosenzweig 1971, p. 385) (i.e. non-persistent) or oscillating herbivore-plant systems as a consequence of positive plant-soil feedbacks are theoretically possible. As plant-soil feedbacks are quite common (Wilson and Agnew 1992), and especially important in semi-arid grazing systems (Graetz 1991), their effects on herbivore dynamics is worth examining. This is yet another area of research that deserves a higher priority on the research agenda.

Practical relevance

Pastoral managers are traditionally concerned with overgrazing and resulting problems of long-term degradation (i.e. reduction of primary and secondary productivity) of their semi-arid rangelands, and equally much attention has been focussed on the rehabilitation of degraded land. The question has arisen whether overgrazing is a proper term or not and whether it should be used in an economic context or in an ecological one (Prins 1989). In some instances it was even concluded that "accusations of overgrazing have typically been poorly defined, unsubstantiated, and based on spot-judgements which themselves relate to standards of range condition inappropriate to semi-arid rangelands and pastoralists/wildlife land use" (Homewood and Rogers 1991, p. 186) and "comments on range degradation by livestock ... have tended to be based on supposition ... rather than objective ecological criteria" (Homewood and Rogers 1991, p. 188). This illustrates that objective ecological criteria are needed on which policy makers and pastoral managers can base their decision how to respond to conditions threatening unfavourable transitions between functional states of semi-arid rangelands.

I think that our approach may eventually lead to such criteria. We mathematically defined five functional states of semi-arid grazing systems depending on the occurrence of soil degradation (i.e. soil erosion by run-off and wind, and the consequent loss of water and nutrients) and grazing: A) undergrazed (type I) state, B) overgrazed state, C) undergrazed (type II) state, D) alternate stable states and E) stably degraded state (Fig. 3) (Chapter 4). Obviously, one functional state may be economically preferred to others (cf. Perrings and Walker 1997), and in terms of pastoral management it is especially important to evade the hazard (cf. Westoby et al. 1989) of passing the highly fluctuating threshold line separating functional state D (alternate stable states) from E (stably degraded state) when coming from functional state C [undergrazed (type II) state] (Fig. 3) (Chapters 3, 4).

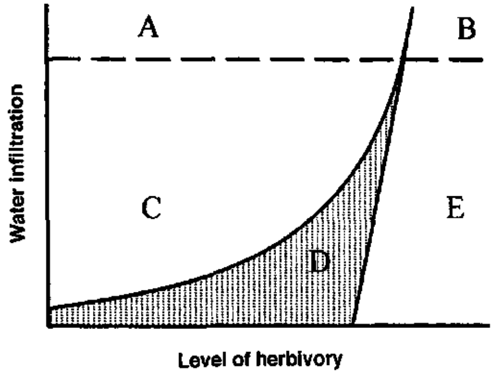

Fig. 3. A parameter plane with a bifurcation set, outlined by the shaded area, defining five functional vegetation states of semi-arid grazing systems, depending on water infiltration and level of herbivory. A = undergrazed (type I) state, B = overgrazed state, C = undergrazed (type II) state, D = alternate stable states, E = stably degraded state. The bifurcation set indicates for which parameter values alternate stable vegetation 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. The location of the bifurcation set fluctuates with rainfall. For further explanation, see Chapter 4.

We showed in our study of multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system (Chapter 6), that an area of intermediate herbivore impact consisted of vegetated patches alternating with bare soil. This area separated an area of high herbivore impact with completely bare soil, from an area of low herbivore impact with a closed vegetation cover, while a positive plants-soil feedback between reduced biomass and reduced water infiltration operated under the conditions investigated. Thus, if it is assumed that variation in space could be interpreted and ordered as a sequence in time (the concept of chronosequence), this indicates that in reality functional state D (alternate stable states) might be revealed by spatial soil and vegetation patterning.

Therefore, a further understanding of soil and vegetation patchiness at different scales and the underlying mechanisms leading to its persistence is practically relevant (cf. Ludwig and Tongway 1995, Schlesinger et al. 1996). It is from these characteristics that pastoral managers can eventually derive criteria on which decisions to evade hazards and to rehabilitate degraded land can be based, and policy makers can finally formulate realistic policies for arid and semi-arid lands. The development and implementation of so-called tracking strategies aimed at timely destocking and restocking of livestock numbers (Toulmin 1994) is essential and should incorporate these above-mentioned criteria. At the same time, the development and implementation of good tracking strategies critically depends on feedback which assesses its success (Stafford Smith 1996). Besides a solid theoretical framework, accurate monitoring and reliable statistics are the basis of long-term successful management strategies.

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Summary

When vegetation is drastically reduced as a result of drought or an increase in herbivore numbers, it does not simply recover if periods with normal rainfall follow or if herbivores are removed. These are commonly recognized catastrophic phenomena of semi-arid grazing systems in general and of the African Sahel in particular. The main aims of this thesis are to provide an effective explanation of the catastrophic properties of vegetation dynamics in these systems and to predict under which conditions they might be expected.

We start with a description of Sahelian rangeland vegetation dynamics, to reveal its catastrophic properties. This exercise appeared a very useful first step in the growth of our ideas about catastrophic vegetation dynamics because: 1) it translated rather vague concepts into a *verifiable format* by deducing hypotheses about the conditions under which catastrophic vegetation dynamics might be expected, and 2) it generated the notion that soil degradation could somehow be an important factor attributing to catastrophic vegetation dynamics in semi-arid grazing systems. This is in contrast with models that emphasize herbivore feeding characteristics or plant competition as possible mechanisms underlying catastrophic vegetation dynamics. We tested the hypothesis that soil degradation, i.e. soil erosion by run-off and wind and the consequent loss of water and nutrients, is sufficient to explain catastrophic vegetation dynamics by mathematical modelling.

Our model studies indeed show that soil degradation can effectively explain the catastrophic properties of semi-arid grazing systems. Soil degradation can cause a positive feedback between reduced resource (soil water and nutrients) availability and reduced vegetation biomass which may lead to collapse of the system. This positive feedback loop can be triggered by grazing. We argue on the basis of a large body of literature that this is an important mechanism causing catastrophic vegetation dynamics in semi-arid grazing systems. Furthermore, our model studies predict for which site-specific properties catastrophic vegetation dynamics may be expected, that is on loamy or clayey soils in case of water-limited vegetation biomass production, and on sandy soils in case of nutrient-limited biomass production. This is because sandy soils have higher water infiltration rates but are more vulnerable to nutrient loss through erosion than loamy or clayey soils.

Based on our models, we hypothesized that the removal of aboveground herbaceous biomass would lead to a reduced soil water content and biomass production because of reduced water infiltration and increased run-off. We tested this hypothesis in a semi-arid savanna in Tanzania (East Africa). Indeed, as a consequence of biomass removal, a reduction in soil water content and biomass production occurred. But it appeared that increased loss of soil water through increased soil evaporation as a consequence of litter removal ultimately outbalanced all other effects on soil water content. Several factors might have contributed to the importance of increased soil evaporation, overriding that of reduced water infiltration and increased run-off. The soil in the research area was a sandy loam, with higher water infiltration rates than soils with a

lower percentage sand and higher perentage clay, while rainfall primarily occurred in light showers. Thus, under these conditions, when the positive feedback between reduced water infiltration and reduced biomass does not operate, another positive feedback that is between increased soil evaporation and reduced biomass may become prominent.

We further hypothesized that at a certain range of herbivore impact small initial differences in plant cover and amount of soil resources can magnify to alternative states which persist in time due to positive plant-soil feedbacks. We tested this hypothesis in a semi-arid grazing system in Burkina Faso (West Africa), where we studied vegetation patchiness along a gradient of herbivore impact. Indeed, the occurrence and likely persistence of a spatial pattern of vegetated patches alternating with bare soil at a certain range of herbivore impact could be explained by the positive plant-soil feedback between vegetation biomass and water infiltration.

We stress the general applicability of our models by comparing catastrophic vegetation dynamics of the semi-arid grasslands of the African Sahel with the arctic salt marshes along the Hudson Bay in Canada. We argue that in both systems, an increase of herbivory triggered a catastrophic vegetation shift, which was ultimately caused by a positive plant-soil feedback, leading to desertification.

One of our model assumptions was that herbivore density is not regulated by vegetation biomass. In the general discussion, I investigated the influence of a positive feedback between vegetation biomass and water infiltration on the dynamics of a plant-herbivore system, where herbivore density depends on vegetation biomass. As a consequence of the positive feedback and if herbivore reproduction is efficient, I predict that the plant-herbivore system could destabilize and collapse. In this chapter I also stress the practical relevance of our studies as our approach may finally lead to objective ecological criteria on which pastoral managers can base their decision how to evade the hazard of degradation of their rangelands.

I highlight three topics which deserve more priority on the reseach agenda concerning semi-arid grazing systems in the near future. Hereby, I want to stress that it is important to put experimental and empirical studies into a clear theoretical framework, whereby mathematical modelling should play an important role. The three topics are:

1) spatial heterogeneity and vegetation pattern formation,
2) facilitation and competition between functional plant groups within the herbaceous layer, and
3) the effects of positive plant-soil feedbacks on herbivore dynamics.

Samenvatting

De vegetatiedynamiek van begraasde, half-droge ecosystemen in het algemeen en van de Sahel in Afrika in het bijzonder kan catastrofale eigenschappen vertonen. De term catastrofaal is hier ontleend aan de catastrofetheorie. Het wil bijvoorbeeld zeggen dat de vegetatie drastisch kan worden gereduceerd als gevolg van droogte of toenemende begrazingsdruk, terwijl het zich niet of slechts langzaam herstelt als vervolgens de regenval normaliseert of de begrazingsdruk afneemt. De belangrijkste doelen van dit proefschrift zijn het verschaffen van een afdoende verklaring van de catastrofale eigenschappen van de vegetatiedynamiek in deze systemen en het voorspellen onder welke omstandigheden ze kunnen worden verwacht.

We beginnen met een beschrijving van de vegetatiedynamiek in de natuurlijke graaslanden van de Sahel in Afrika. Hierbij wordt met name aandacht besteed aan de catastrofale eigenschappen van die vegetatiedynamiek. De bovengenoemde beschrijving bleek zeer nuttig te zijn, omdat we hierdoor testbare hypotheses konden afleiden over de omstandigheden waaronder deze catastofale eigenschappen kunnen worden verwacht. Door deze beschrijving kwamen we ook op het idee dat bodemdegradatie (erosie door afstroming van regenwater en wind en de daarmee gepaard gaande verliezen van water en nutrienten) wel eens een belangrijke factor zou kunnen zijn die dergelijke eigenschappen zou kunnen verklaren. Dit is tegenstrijdig met de huidig gangbare verklaringen, die meer de nadruk leggen op het graasgedrag van herbivoren en op de concurrentie tussen planten. De hypothese dat bodemdegradatie een afdoende verklaring is voor de catastrofale eigenschappen van de vegetatiedynamiek in half-droge, begraasde ecosystemen hebben we vervolgens getest door middel van wiskundige modellen.

Deze modelstudies laten inderdaad zien dat bodemdegradatie een afdoende verklaring is. Bodemdegradatie kan een positieve feedback veroorzaken tussen een lagere beschikbaarheid van bodemwater en -nutrienten en een verminderde vegetatiebiomassa, wat kan leiden tot een negatieve spiraal, waardoor het systeem als het ware in elkaar stort. Deze negatieve spiraal kan in beweging worden gezet door begrazing. We stellen dan ook dat dit een belangrijk mechanisme is wat catastrofale vegetatieveranderingen veroorzaakt in begraasde, half-droge ecosystemen. Verder voorspellen we met behulp van onze modellen dat catastrofale vegetatieveranderingen kunnen worden verwacht voor lemige en kleiige bodems als de vegetatieproductie wordt beperkt door de beschikbaarheid van bodemwater en voor zandige bodems als de vegetatieproductie wordt beperkt door de beschikbaarheid van bodemnutrienten. Dit komt omdat zandige bodems een hogere infiltratiecapaciteit hebben dan lemige of kleiige bodems, maar tegelijktijd gevoeliger zijn voor nutrientenverliezen als gevolg van erosie.

Van bovengenoemde modellen hebben we vervolgens de hypothese afgeleid dat de verwijdering van bovengrondse biomass zal leiden tot een lagere beschikbaarheid van bodemwater en een lagere vegetatieproductie, door een lagere infiltratie van regenwater in de bodem en daarmee een toename van de afstroming. Deze hypothese hebben we getest in een savannegebied in Tanzania (Oost-Afrika). We vonden daar inderdaad een afname van bodemvocht en biomassaproductie als gevolg van de verwijdering van bovengrondse biomassa. Maar het effect van de toename van de bodemevaporatie als gevolg van het weghalen van strooisel overtrof het verwachte effect van de afname van infiltratie en toename van afstroming. Een mogelijke verklaring hiervoor is dat de bodem in het onderzoeksgebied zandig leem was, waarin over het algemeen meer water kan infiltreren per tijdseenheid dan in bodems met een lager zand- of hoger kleigehalte. Verder bestond de neerslag hoofdzakelijk uit lichte regenbuien. Dus de mogelijkheid bestaat dat een positieve feedback tussen een lagere beschikbaarheid van bodemwater door hogere bodemverdamping en een lagere vegetatiebiomassa belangrijk wordt, wanneer de omstandigheden zodanig zijn dat een positieve feedback tussen een lagere infiltratie van regenwater en een verminderde vegetatiebiomassa niet optreedt.

Onze modellen voorspellen ook dat kleine verschillen in vegetatiebedekking en en in hoeveelheid bodemvocht en -nutrienten kunnen divergeren tot uiteenlopende, stabiele toestanden als gevolg van positieve plant-bodem feedbacks. Deze positieve plant-bodem feedbacks en de daarmee gepaard gaande uiteenlopende vegetatietoestanden zouden dan tot uiting moeten komen voor een bepaald interval langs een begrazingsgradient. In Burkina Faso (West-Afrika) hebben we deze hypothese getest. We vonden inderdaad een zone waar vegetatie en kale bodem elkaar afwisselden in een min of meer regelmatig patroon langs een begrazings- en vertrappingsgradient. Hier konden we aantonen dat meer regenwater kon infiltreren in door vegetatie bedekte bodem dan in de kale, kleiige grond. Hierdoor stroomde er minder regenwater af van de plekken met vegetatie dan van de kale plekken. De vorming en waarschijnlijke stabiliteit van een dergelijk patroon kon dus afdoende verklaard worden door de werking van een positieve feedback tussen vegetatiebedekking en infiltratie van regenwater.

We vergelijken de catastrofale eigenschappen van de vegetatiedynamiek van de natuurlijke graaslanden van de Sahel in Afrika met die van de arctische kwelders langs de kust van de Hudson Bay in Canada. Hierdoor benadrukken we de algemene toepasbaarheid van de inzichten die onze modellen genereren. Een toename van de begrazingsdruk ging in beide systemen gepaard met een catastrofale vegetatieverandering en uiteindelijk zelfs verwoestijning, waarvan de eigenlijke oorzaak kan worden gevonden in het optreden van positive plant-bodem feedbacks.

Eén van de veronderstellingen in onze modellen is dat de dichtheid van herbivoren niet wordt gereguleerd door vegetatiebiomassa. In de algemene discussie onderzoek ik met behulp van een model de invloed van een positieve feedback tussen vegetatiebiomassa en infiltratie van regenwater op de dynamiek van een plant-herbivoor systeem, waarbij de dichtheid van de herbivorenpopulatie afhangt van de vegetatiebiomassa. Het model voorspelt dat een plant-herbivoor systeem kan destabiliseren en zelfs in elkaar kan storten als gevolg van deze positieve plant-bodem feedback, wanneer de reproductie van herbivoren efficiënt is. Ik benadruk ook de praktische toepassing van ons onderzoek. Onze onderzoeksbenadering kan uiteindelijk leiden tot objectieve ecologische kriteria op basis waarvan beheerders hun beslissingen kunnen nemen om het gevaar van degradatie van hun natuurlijke graaslanden te vermijden.

Ik onderscheid drie belangrijke onderzoeksgebieden ten aanzien van half-droge, begraasde ecosystemen die meer prioriteit verdienen. Hierbij wordt benadrukt dat veldexperimenten en empirische studies geplaatst dienen te worden in een helder theoretisch kader, waarbij modelwerk belangrijk is. Deze onderzoeksgebieden zijn:

1) ruimtelijke verscheidenheid en vegetatiepatroonvorming,

2) facilitatie en concurrentie tussen functionele plantengroepen binnen de kruidlaag en

3) de effecten van positieve plant-bodem feedbacks op de dynamiek van herbivorenpopulaties.

Curriculum vitae

Max Rietkerk (1966) was born in Maassluis (The Netherlands). He followed secondary school in Maassluis from 1978 to 1982 (MAVO) and in Rotterdam from 1982 to 1984 (HAVO). From 1984 he studied at the Advanced College for Forestry and Land and Water Management in Velp (The Netherlands), where he graduated (Ing. degree, equivalent to B.Sc.) in 1988. Directly after this study he worked during a period of three months as a research assistant at the Agricultural Research Organisation, Institute of Soils and Water, Department of Environmental Physiology and Irrigation in Bet Dagan (Israel). Here, he was responsable for the operation of an experimental drip irrigation system close to the Negev desert providing saline ground water and fresh surface water to cotton plants, and for various soil and vegetation measurements. He then worked from 1988 to 1990 at the Ministery of Agriculture, Nature Management and Fisheries, Land Development Service in Maasland (The Netherlands), where he prepared and supervised various technical and financial aspect of land development projects in horticultural areas.

Due to lack of scientific challenge and eager to learn more about ecology and land use, he decided to resign from this job in 1990 and to study at Wageningen Agricultural University (The Netherlands). Field work for his first graduation thesis took him to Burkina Faso where he studied soil variability and the effectiveness of some soil conservation measures during a period of four months. For his second graduation thesis, he studied the collections of Caesalpinioideae trees in the herbaria of Wageningen, Brussels and Paris, in order to relate their distribution in Central Africa to forest refuge theory. He graduated (Ir. degree, equivalent to M.Sc.) *cum laude* in 1993, with special reference to Land and Water Use.

From 1993 to 1994 he was appointed as a research assistant at Wageningen Agricultural University, Department of Terrestrial Ecology and Nature Conservation. During this period he assisted in education and research, and he prepared his research proposal for his doctoral study. From 1994 until 1998 he worked as a researcher in training (AIO) at Wageningen Agricultural University, Department of Environmental Sciences, Erosion and Soil and Water Conservation Group. It was during this period that he carried out the research resulting in this doctoral thesis, in close co-operation with the Tropical Nature Conservation and Vertebrate Ecology Group from the same department and university. From 1993 to 1994 he was also a member of the board of the "Evert Vermeer Stichting", the national PvdA (Labour Party) foundation for international solidarity, and from 1993 to 1997 he was board member of "Montañas Verdes", a foundation for nature conservation and sustainable land use in the Andes region of Latin America.