An integrated modelling approach for sustainable management of semi-arid and arid rangelands

Ph.D. Thesis

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1 Summary

The need to develop sustainable resource management strategies for semi-arid and arid rangelands is acute as non-adapted grazing strategies lead to irreversible environmental problems such as desertification and associated loss of economic support to society. In such vulnerable ecosystems, successful implementation of sustainable management strategies depends on well-founded understanding of processes at different scales that underlay the complex system dynamic. There is ample evidence that, in contrast to traditional sectoral approaches, only interdisciplinary research does work for resolving problems in conservation and natural resource management. In this thesis I combined a range of modelling approaches that integrate different disciplines and spatial scales in order to contribute to basic guidelines for sustainable management of semi-arid and arid rangelands.

Since water availability and livestock management are seen as most potent determinants for the dynamics of semi-arid and arid ecosystems I focused on (i) the interaction of ecological and hydrological processes and (ii) the effect of farming strategies.

First, I developed a grid-based and small-scaled model simulating vegetation dynamics and interlinked hydrological processes. The simulation results suggest that ecohydrological interactions gain importance in rangelands with ascending slope where vegetation cover serves to obstruct run-off and decreases evaporation from the soil. Disturbances like overgrazing influence these positive feedback mechanisms by affecting vegetation cover and composition.

In the second part, I present a modelling approach that has the power to transfer and integrate ecological information from the small scale vegetation model to the landscape scale, most relevant for the conservation of biodiversity and sustainable management of natural resources. I combined techniques of stochastic modelling with remotely sensed data and GIS to investigate to which extent spatial interactions, like the movement of surface water by run-off in water limited environments, affect ecosystem functioning at the landscape scale. My simulation experiments show that overgrazing decreases the number of vegetation patches that act as hydrological sinks and run-off increases. The results of both simulation models implicate that different vegetation types should not only be regarded as provider of forage production but also as regulator of ecosystem functioning. Vegetation patches with good cover of perennial vegetation are capable to catch and conserve surface run-off from degraded surrounding areas. Therefore, downstream out of the simulated system is prevented and efficient use of water resources is guaranteed at all times. This consequence also applies to commercial rotational grazing strategies for semi-arid and arid rangelands with ascending slope where non-degraded paddocks act as hydrological sinks.

Finally, by the help of an integrated ecological-economic modelling approach, I analyzed the relevance of farmers' ecological knowledge for longterm functioning of semi-arid and arid grazing systems under current and future climatic conditions. The modelling approach consists of an ecological and an economic module and combines relevant processes on either level. Again, vegetation dynamics and forage productivity is derived by the small-scaled vegetation model. I showed that sustainable management of semi-arid and arid rangelands relies strongly on the farmers' knowledge on how the ecosystem works. Furthermore, my simulation results indicate that the projected lower annual rainfall due to climate change in combination with non-adapted grazing strategies adds an additional layer of risk to these ecosystems that are already prone to land degradation.

All simulation models focus on the most essential factors and ignore specific details. Therefore, even though all simulation models are parameterized for a specific dwarf shrub savannah in arid southern Namibia, the conclusions drawn are applicable for semi-arid and arid rangelands in general.

2 General Introduction

1. Relevance

Our environment largely consists of human-influenced ecosystems, managed to varying degrees, in which the natural services that humans depend on becomes harder and harder to maintain. One key aim for the 21st century is therefore "sustainable development," which the international community embraced at the 1992 UN Conference on Environment and Development (UNCED). In general, from a human point of view, sustainability means nothing more than using natural resources no faster than they can regenerate themselves (Merkel 1989, McMichael et al. 2003). For semi-arid and arid rangelands sustainability is understood as the maintenance of the long-term productivity of the vegetation whilst simultaneously providing sufficient income for the land user (Pickup and Stafford Smith, 1993). Particularly for these ecosystems, the need to implement and continually update sustainable resource management strategies plays a decisive role: First, they cover about a third of the world's land surface, occur in all continents and are inhabited by at least one billion people or approximately 20 % of the total world population which rely basically on small stock farming (UNCCD 2004, Sivakumar et al. 2005). Second, alone on the African continent two third of the semi-arid and arid regions are affected by land degradation due to non-adapted grazing strategies (UNEP 1994, UNO 2002). Third, a reduction in mean annual rainfall as predicted by climate models for the subtropical latitudes (Easterling et al. 2000, IPCC 2001) will likely lead to a general decrease in the grass resource and increased vulnerability of dryland to degradation.

There is ample evidence that traditional sectoral, disciplinary approaches do not work to attain sustainability for such vulnerable ecosystems (e.g. Krausmann et al., 2004, Haberl et al. 2006). Increasingly, interdisciplinary research is acknowledged as essential for resolving problems in conservation (Deem et al. 2001, Stem et al. 2005) and natural resource management (Daily and Ehrlich 1999) as maintenance of ecosystem services will require a considerably better understanding of processes that sustain them at different scales.

In semi-arid areas, rangelands livestock management and water availability are widely seen as most potent determinants for ecosystem functioning (Fynn and O'Connor 2000). Nevertheless, until now the impact of both factors that underlay the system's dynamics is not completely understood and it principally remains unclear how they interplay.

Soil water availability acts as controlling resource for ecosystem functioning by triggering vegetation processes like establishment and productivity. Generally, the capability of landscapes to store water is related to feedback mechanisms between hydrological processes and vegetation. Despite the awareness of these soil-plant feedback mechanisms our knowledge is still poor and recent cri-

tiques have emphasized the need for more research at the interface of ecology and hydrology (e. g. Rodriguez-Iturbe 2000, Ludwig 2005).

Land utilization by domestic livestock can lead to a reduction of palatable grasses and herbs coupled with shrub encroachment or desertification. This shift has been shown to be accompanied by reductions in primary productivity. Management of ecosystems is a process of land-use decision that takes into account the full suite of organisms and processes that characterize and comprise the ecosystem and is based on the best understanding currently available how the ecosystem works. It therefore is regarded as one of the greatest environmental challenges (Millennium Ecosystem Assessment 2005). But although present-day ecology has broadened its perspectives significantly, there is still a tendency to exclude consideration of both human influence and dependence on ecosystem dynamics.

2. Objectives

In this thesis I aim to contribute to basic guidelines for sustainable management of semi-arid and arid rangelands. Exemplary, I investigate grazing systems in a dwarf shrub savannah in arid southern Namibia (Figure 1). To fill the gaps highlighted in the previous paragraph, a comprehensive understanding of processes at different scales that underlay the complex system dynamic of semi-arid and arid rangelands is a prerequisite. Simulation models play a significant role to get a reasonably rich picture for several reasons: First, models are important tools to integrate parameters and processes of different disciplines in a consistent way, thus aiding interdisciplinary analyses and providing an understanding of the key factors of the system dynamics. Second, extrapolation of information across spatial and temporal scales provides difficulties, which can directly affect the accuracy of predictions (Levin 1992, Heuvelink 1998, Clark et al. 2001). Modeling tools have the power to project knowledge derived from short-term studies on small plots to regional and global scales to explore dynamics over long time periods (Briske et al 2003). Third, decision-making processes in management and politics need models that demonstrate the consequences of different decisions and can be of great help in an interactive process between researchers and stakeholders. I combined a range of integrative modelling approaches that help to provide a basis for recommendations for more sustainable grazing practices in these complex systems.

One model simulates vegetation dynamics and interlinked hydrological processes at small spatial scales where the underlying ecological processes e.g. local water availability, triggering germination rates and plant growth are best understood. In contrast, decisions for the conservation of biodiversity and sustainable management of natural resources are made for long time periods and at large spatial scales (Peters et al. 1997, Miller et al. 2004). However, extrapolation of information
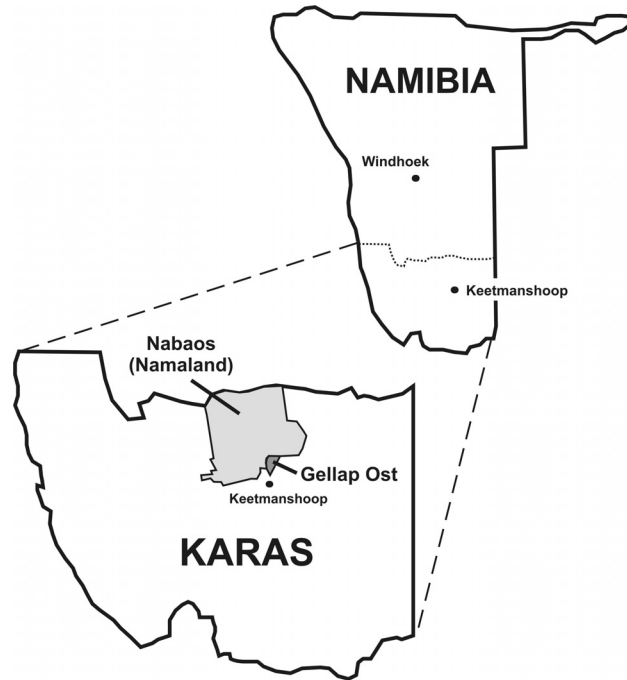
Figure 1: Location of the two case studies commercial research farm Gellap Ost and communal rangeland Nabaos

across scales provides difficulties as we do not know to which extent spatial interactions, like the movement of surface water by run-off in water limited environments, affect ecosystem dynamics at large spatial scales (Levin 1992, Wootoon 2000, Strayer 2003, Urban 2005). Omission of these processes may directly affect the accuracy of predictions (Heuvelink 1998, Weaver and Perera 2004). Therefore, I used a combined technology of remote sensing, GIS and stochastic modelling that incorporates lateral exchange of surface water to transfer and integrate ecological information from the small scale to the landscape scale.

Finally, by the help of an integrated ecological-economic modelling approach, I analyzed the relevance of a farmers' ecological knowledge on how the ecosystem works for longterm functioning of grazing systems. Generally, sustainable management of semi-arid and arid savannas is achieved by good farmers' ecological knowledge. Therefore, land-use decision making should take the full suite of ecological processes that characterize and comprise the ecosystem into account and should be based on the best understanding currently available how the ecosystem works (Dale et al. 2000, Olsson and Folke 2001, Gunderson and Holling 2002, Olsson et al. 2004). However, there is a great mismatch between the kinds of ecosystems that farmers want and the kinds of ecosystems that are attainable (Carpenter and Gunderson 2001): Farmers tend to overestimate the biomass available for grazing at a certain amount of annual rainfall as they ignore ecological expertise to serve narrow interest like short-term income. Such non-adapted grazing strategies may lead to irreversible environmental problems like desertification and associated loss of economic support to society (UNEP 1995). The modelling approach consists of an ecological and an economic module. The economic module is based on knowledge of a previously built detailed linear optimization

model (Domptail et al. submitted). The ecological module is used to simulate the impact of the farmers' land-use decision, derived by the economic module, on ecosystem dynamics and resulting carrying capacity of the system for livestock under current and future climatic conditions.

To guarantee that data collected and processes estimated at smaller spatial scales are included, ecological processes for both, the landscape modelling approach and the ecological-economic modelling approach are derived by the small-scaled vegetation model.

3.   Structure of the thesis

This thesis consists of three major chapters that cover the work of my dissertation research. All chapters have been written as independent papers to be submitted to international scientific journals in cooperation with co-authors. Remotely sensed data for chapter 4 was provided by Melanie Vogel, by the time of the study member of DLR - German Aerospace Center. The linear optimization model used in chapter 5 was implemented by Stephanie Domptail, by the time of the study member of the Institute for Agrarcultural Policy and Market Research, University of Giessen. Nonetheless, all findings presented in this thesis are the result of work that has been done independently by myself. The idea to publish every single chapter is the reason why this thesis has been written in the first person plural. The chapters can be read independently and are linked by a short summary and outlook on the proceeding chapter. Therefore, a certain amount of repetition in model description and description of the research area does emerge.

In the first chapter, I investigate the relative impact of small scale soil-plant interactions on vegetation dynamics. Thereafter, in the second chapter, I present a simulation tool which has the power to transfer ecological small-scale information and processes to larger spatial scales. Combining technologies of remote sensing and stochastic modelling, I demonstrate the impact of surface water flow on vegetation dynamics, composition and productivity at the landscape scale. In the third chapter, I present an integrated ecological-economic approach that consists of an ecological and an economic module and combines relevant processes on either level. Based on this I investigate the importance of farmers' knowledge in times of climate change. At the end, I conclude the thesis with a general discussion and outlook and a German summary.

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3 Ecohydrological feedback mechanisms in arid range-lands: Simulating the impacts of topography and landuse [1]

1. Abstract

Particulary in arid and semi-arid regions ecological and hydrological processes can interact. Often the interaction of these processes is not completey understood and mostly studied seperately. We developed a grid-based computer model simulating the population dynamics of the four most abundant vegetation types (perennial grass, annuals, dwarf shrubs and shrubs) and interlinked hydrological processes. These ecohydrological interactions gain importance in rangelands with ascending slope where vegetation cover serves to obstruct run-off and decreases evaporation from the soil. Disturbances like overgrazing influence these positive feedback mechanisms by affecting vegetation cover and composition. In this study we first show that model predictions of cover and productivity of the vegetation types are realistic by comparing model output with cover and productivity estimates obtained from field surveys. Subsequently, we apply a realistic range of slope angle combined with 2 landuse regimes (high versus low grazing intensity).

Based on the simulation results we suggest that the sensitivity of ecosystem functioning to topography is strongly affected by disturbances like overgrazing. Low stocking rates maintain undisturbed vegetation, low values of run-off and evaporation at gentle slope. Nevertheless, at steeper slopes water retention potential decreases leading to lower productivity and higher levels of run-off and evaporation. In contrast, overgrazing reduces vegetation cover, biomass production and composition whereas the landscape becomes less efficient at trapping run-off, leading to high losses of water even in landscapes with less steeper slopes. Abundance of perennial grass as well as dwarf shrubs decreases with increasing slope angle as well as grazing pressure and dominance is shifted towards shrubs and annuals. As a management recommendation we suggest that different vegetation types should not only be regarded as provider of forage production but also as regulator of ecosystem functioning. Particulary on rangelands with ascending slope, good cover of perennial vegetation patches guarantees that water does not leave the system and cause rapid losses in forage production due to artificial droughts.

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2. Introduction

In arid and semi-arid regions inappropriate land use practices lead to land degradation, reducing biological and economic productivity (UNEP 1994). Here, soil water availabity acts as controlling resource for ecosystem functioning and organization by triggering vegetation processes like establishment and productivity (e.g. Sanchez and Puigdefabregas 1994, Seghieri and Galle 1999, Rodriguez-Iturbe 2000). Generally, the capability of landscapes to store water is related to soil texture (Ludwig et al. 2005) as well as to feedback mechanisms between hydrological processes and vegetation (Cammeraat and Imeson 1999, Wilcox et al. 2003). In flat and undisturbed landscapes local soil water availability is determined by precipitation (Jobbagy et al. 1996) whereas in landscapes with distinct topography rainfall gets redistributed by overland transport of water by run-off (Cammeraat and Imeson 1999, Wilcox et al. 2003). However, the redistribution of water depends on multiple and complex processes based on coupled and non-linear dynamics such as plant-soil interactions (Bergkamp 1998).

These mechanisms have been described by the trigger-transfer-reserve-pulse (*TTRP*) conceptual framework (Ludwig et al 1997, Ludwig et al. 2005) where run-off occurs if rainfall intensities exceed soil infiltration capacities. Infiltration rates are sensitive to changes in slope angle as flow velocity increases at steeper gradients (Chaplot and Bissonnais 2000, Joel et al. 2002, Wilcox 2003). Additionally, vegetation acts as surface obstruction, increases soil structure and aggregation (Ludwig et al. 2005). Thus, infiltration rate is positively correlated with vegetation cover and biomass (Bergkamp 1998, Cerda 1998). Furthermore, plant cover reduces evaporation of soil water by reducing surface temperatures (Domingo et al. 2000, Puigdefabregas 2005). Disturbances such as heavy grazing may disrupt these fragile plant-soil interactions (Schlesinger et al. 1990, Wilcox 2003). Grazing and trampling of livestock leads to a reduction of plant cover and biomass resulting in increased runoff and high evaporation rates. This may lead to a change in vegetation structure and spatial redistribution of soil water availability.

Despite the awareness of these soil-plant feedback mechanisms our knowledge on the strength and extent of the impact of topography and landuse on vegetation and hydrological dynamics is still poor. Therefore, recent critiques have emphasized the need for more research at the interface of ecology and hydrology (Rodriguez-Iturbe 2000, Ludwig 2005). Simulation models seem to be an important tool to incorporate interactions among precipitation and disturbances like grazing into ecohydrological dynamics across spatial and temporal scales. However, until now, most models considering plant-soil interactions are unrealistically oversimplified. First, models generally use aggregated precipitation for predicting runoff, but negate frequency, magnitude, and timing of runoff (Wilcox 2003). Moreover, not only the temporal but also the spatial dynamics are disregarded.

Very few studies have attempted to describe how naturally produced runoff at the vegetation-patch scale relates to runoff at the hill-slope scale (Rodriguez-Iturbe 2000). In this study, we developed a grid-based model *TOPMAN* (TOPographical MANagement) to investigate the relative impact of small scale soil-plant interactions on vegetation dynamics in a semi-arid dwarf shrub savanna in southern Namibia. The model simulates the vegetation dynamics of the four most abundant vegetation types (perennial grass, forbs, dwarf shrubs and shrubs) and explicitly includes topography and hydrological processes (on intra-, and interannual time scales). The model is applied to 2 landuse regimes (high versus low grazing impact) to test for (i) the effect of landuse and (ii) the importance of topography on aboveground biomass production. To gain a mechanistic understanding of the importance of topography we systematically investigated the impact of slope under low and high impact of grazing. We validated the model by comparing the model output with cover estimates of the perennial and productivity of the herbaceous vegetation obtained from field surveys in the research area. Detailed knowledge of processes concerning the limiting soil water resource is essential in times of climate and landuse change (Fynn and O'Connor 2000, Wilcox 2003, Ludwig et al. 2005). The results will help to improve the management and sustainable use of arid and semi-arid pastures with distinct topography.

3.   Methods

3.1.   Study area

The study region is located in the Nama-Karoo in southern of Namibia. Rainfall throughout the entire region is erratic and highly variable with a mean of 150 mm. It often occurs as isolated thunderstorms (Heyns et al 1998). High evaporation rates are measured due to high daytime temperatures up to 37° C (Namibian Meterological Service 2000). The main topografical features of the two study areas Gellap Ost (low grazing impact) and Nabaos (high grazing impact) are flat regions, as well as regions with gentle and precipitous slopes (Kuiper and Meadows 2002). The Nama-Karoo vegetation is greatly restricted by these geophysical characteristics and strongly depends on rainfall. Vegetation cover is low and when heavily grazed, perennial grasses (e.g. *Stipagrostis spp.*) greatly valued as forage are replaced by annual grasses (e.g. *Schmidtia kalahariensis*) and unpalatable shrubs (e.g. *Rhigozum trichtomotum*) (Kuiper and Meadows 2002). Main resource use activity in the communal area as well as at the Gellap Ost Research Station is small stock farming. Gellap Ost has 160 purposely under-stocked camps, where animals graze in rotational system. Resting periods of camps (without grazing) of at least one year per camp prevent overgrazing (Kuiper and Meadows 2002). In contrast, the communal farming land is managed under a communal land tenure system wherein livestock movement in the area is not controlled and overstocking has strong impact on the rangeland resource.

3.2. Model description

3.2.1. General model structure

We developed a spatially-explicit and individual-based model to investigate the impact of small scaled plant-soil interactions in a water limited environment. The model is composed of four hierarchical levels: vegetation (lowest level), cell, landscape and abiotic environment (highest level).

Vegetation - The model simulates two herbaceous vegetation types perennial grass and annuals and six types of woody vegetation. Woody vegetation is distinguished by height (shrubs and dwarf shrubs). Trees are relatively rare in the research area and are exluded from this study. All vegetation types differ in their ability for establishment (dispersal and seed persistence), productivity, palatability and resistance to disturbance.

Cell – Cell size is 3 m x 3 m and corresponds to the maximum diameter of a shrub. Cells can consist of bare ground, perennial grass, annuals or woody plant individuals whereas a combined occupation of several vegetation types is possible. Perennial grasses and annuals are treated as matrix plants, and a cell is either occupied or not. Woody plants are attributed individually for each cell and included in a cell specific attribute list. We assigned elevation values for each cell, related infiltration rates to soil texture, vegetation cover and slope. Evaporative demand is based on soil texture as well as local micro-climate affected by vegetation cover.

Landscape - Cells are linked with each other by means of a grid based structure with the size of 1 ha. The model landscape is implemented to capture the three most abundant topographical features of the area: flat (*TF*), gentle slope (*TG*) and precipitous slopes (*TP*). The topgraphical features *TG* and *TP* are characterized by decreasing elevation values of the cells towards one side of the landscape.

Abiotic environment - The highest level of the model is the abiotic environment. In arid ecosystems water availability is discontinuously available influencing the ecosystem as discrete pulse events interspersed among long periods of limited resource availability (Sala and Lauenroth 1982). To consider these biologically important rainfall events water availability affects simulated vegetation dynamics on an hourly, monthly and annual base.

The model proceeds in annual time steps. Within each time step, the model-modules are processed as follows: water availability, growth, grazing, establishment and mortality. In the following we give an overview of these modules, detailed description is attached as Appendix (A).

3.2.2. Overview of simulated processes

Water availability - Cell-specific water availability of the different vegetation types is influenced by rain, run-off, evaporation and competition. Run-off occurs primarily as infiltration-excess overland flow from high elevations to low-levelled areas, controlled by infiltration characteristics (Wilcox et al. 2003). Infiltration rates are related to the cells soil texture (HilleRisLambers et al. 2001),

vegetation cover (Battany 2000) and slope (Chaplot and le Bissonnais 2000). Moreover, soil texture and vegetation cover have an impact on evaporation (Le Houerou 1984, Snyman 2000), reducing soil water content in the upper soil layer. Competitive effects of vegetation reduce the water availability for establishment and, in cells with overlapping root systems vegetation has a competitive effect on the neighbouring vegetation types (Callaway 1997).

Establishment - In arid and semi-arid environments sufficient moisture (O'Connor 1996) and the occurrence of seeds (Milton 1994, O'Connor and Picket 1996) are the main conditions for successful establishment. Furthermore, little food for livestock heightens trampling effects and the probability that livestock feeds on the seedlings (Danckwerts and Stuart-Hill 1988, Milton 1994, Carrick 2003). So, the cells' probability of successful establishment for the perennial vegetation (woody plants and perennial grasses) is determined by site-specific probabilities of seed and water availability as well as the probability to survive grazing. Annuals, producing large numbers of seeds and persistent seed banks (Jackson and Roy 1986, Veenendaal 1996) are only restricted by water availability and grazing pressure.

Growth - Biomass production of the herbaceous vegetation is related to annual water availability of the two matrix plant types annual and perennial grass. For both vegetation types, we use a growth coefficient derived from rainfall-grass production relationships of divers southern African savanna regions (Higgins 2000). In contrast, annual biomass production of woody plant individuals depends on impacts of water availability and current height performance.

Grazing – The model simulates grazing and browsing on herbaceous and woody vegetation. Vegetation types differ in their palatability for grazers and browsers. What and to which amount a plants biomass will be consumed depends on the relation of available and needed forage as well as its specific palatability.

Mortality - Survival of perennial plants is environmentally determined by the availability of water and the impact of grazing by livestock (O'Connor 1994, Fensham and Holman 1999, Milton and Dean 2000). We related the probability to survive to the plants performance, since disturbances as drought or overgrazing have strong influence on productivity. Within the group of perennial plants differences among species in disturbance tolerance results in better physiological adaptations to disturbance.

3.3. Validation

We validated the model by comparing the model output with cover estimates of the productivity of perennial and herbaceous vegetation obtained from field surveys in the year 2001 (Prinsloo and Bester 2003, Wolkenhauer 2004). If available, we compared field patterns and model output for the low grazing area Gellap as well as the high grazing area Nabaos. Field surveys were conducted on landscape level and not related to topographical feature. Thus, the impact of topography has been

obliterated. Therefore, we assume the simulation model to represent realistic vegetation dynamics and productivity if the mean respective mean output of topographical features without slope and topographical features with 5 % of slope lies in between measured data. Here, we excluded slopes of 20 % as we suppose that these topographical features did not affect field data due to their low occurrence in the research area.

3.4. Simulation experiments

With the model presented here we intend to evaluate the effect of topography on vegetation and linked hydrological dynamics under the different grazing history of low grazing impact at Gellap Ost and high grazing impact at Nabaos. In doing so, we show the effect on cover and productivity of the main vegetation types perennial grass, annuals, dwarf shrubs and shrubs as well as runoff and evaporation for the three identified topographical features flat (*TF*), gentle (*TG*) and precipitous (*TP*) (Kuiper and Meadows 2002) with slopes of 0%, 5% and 20%. Then, we will summarize the impact on ecosystem functioning by estimating the impact of topography and management method on water use efficiency for the realistic range of slope (0 – 30 %).

The spatial and temporal vegetation and hydrological dynamics is presented for 50 years. For model initialisation we used the vegetation structure of an undisturbed dwarf shrub savanna. Since little is known about this vegetation structure we assumed an undisturbed coexistence of perennial grasses, dwarf shrubs and shrubs. Thus initial vegetation conditions are 50% of perennial grass cover, 30% of dwarf shrub cover and 20% of shrub cover. Plants are distributed randomly over the grid. Before the model analysis started, the simulation was run for 150 time steps to exclude initialisation effects. Beginning with semi-nomadic herding of the Nama people (Kempf 1994) the stocking rate (given in Small Stock Unit = SSU) was set to 0.015 SSU / ha. Due to the arrival of European colonialists in 1885 farmers settled down and stocking rate increases to 0.05 SSU / ha. Gellap Ost remained under commercial tenure and changed in 1960 into a research farm with 160 purposly under-stocked camps, allowing a rotational grazing system. In contrast, Nabaos changed to communal land with no boundary fences and resulting continuous grazing at stocking rates of 0.2 SSU / ha. As rainfall data for the whole time series of 200 years are lacking, we repeatedly stringed a sequence of monthly precipitation for the years 1945-2000 together (Namibian Metereological service 2000). For the purpose of keeping track to effects we only show simulated data for the last rainfall sequence from 1948 to 2002. Due to the stochastic processes in the model, no single run is representative. Therefore, we started 500 repeats for each scenario.

Statistical analysis – We applied the program SPSS (version 11.0.1, 2001) for statistical analysis. Possible relationships between annual precipitation and phytomass production as well a hydrologi-

cal processes and phytomass production were analyzed by regression models with linear fit. We further estimated the impact of slope and management by a 2-factorial ANOVA.

3.5. Sensitivity analysis

For the sensitivity analysis we compared water use efficiency (*WUE*) of modified parameters with WUE for the standard parameter set. *WUE* is defined as *B / R,* where *B* is annual total biomass production (kg DM ha^{-1}) and *R* is annual rainfall (mm) (Le Houerou 1984). Thereby we could identify key model parameters and assess the effects of parameter uncertainty. Based on field data and literature we created a default parameter set for the *TOPMAN* model. Each parameter was modified by ±10% of its default value while keeping all other parameters constant (Wichmann 2003, Rossmanith et al. 2006). Thus, the sensitivity of each parameter was investigated separately.

For each parameter set, the model was run 1000 times for the grazing history of the last 200 years for the low grazing (Gellap) and the high grazing scenario (Nabaos) and, to guarantee response of all parameters, the landscape feature slope. Sensitivity is calculated as the relative change of *WUE* divided by the relative change of the respective parameter.

$$SI = \frac{\dfrac{\Delta WUE}{WUE}}{\dfrac{\Delta P}{P}} \tag{1}$$

The higher the absolute value of *SI*, the higher the sensitivity of this parameter. Due to the high number of parameters we simplified the analysis by grouping. To evaluate the importance and sensitivity of the main model processes concerning the impact of vegetation on the conservation of soil water, remaining processes determining water availability, growth, establishment and mortality we grouped the parameters based on the main processes they belong to.

4. Results

4.1. Validation

Simulation results show that shrub cover and productivity for the year 2001 matched with the field survey for the low and the high grazing scenario (Table 1). Even though availability of field data is low we are confident that the model grasps the most important vegetation dynamics and linked hydrological processes.

Table 1: Validation. Mean model output (*mean*) for scenarios without topography (*flat*) and *gentle slope* is compared with cover estimates (*C*) of perennial grass, dwarf shrubs and shrubs as well as productivity (*P*) of perennial grass and annuals obtained from field surveys in the year 2001 at research sites with low (*L*) and high grazing intensities (*H*). See text on validation for further description.

	Scenario	Shrub	Dwarf shrub	Perennial grass	Annuals
P_L	*flat*	-	-	*305*	*71*
	gentle slope	-	-	*259*	*63*
	mean	-	-	274	67
	field survey	-	-	258	56
C_L	*flat*	*59*	*41*	*62*	-
	gentle slope	*54*	*47*	*50*	-
	mean	57	43	55	-
	field survey	60	40	50	-
C_H	*flat*	*84*	*16*	*2*	-
	gentle slope	*100*	*0*	*0*	-
	mean	92	8	1	-
	field survey	80	19	1	-

4.2. Simulation Results

Total Phytomass and precipitation - In all scenarios, annual total phytomass production was affected by annual precipitation (Figure 1). The range of annual precipitation for the simulated years was 58 – 512 mm. Annual phytomass production in this time-span ranged from 1200 kg ha^{-1} to 0 kg ha^{-1}. Phytomass was regressed against precipitation, slope and management method. At the low grazing scenario, the slope of the regression line between phytomass and precipitation was 3.6 kg ha^{-1} mm^{-1} for flat areas *TF* ($R^2 = 0.91$, $p < 0.001$), 2.6 kg ha^{-1} mm^{-1} for gentle slopes *TG* ($R^2 = 0.81$, $p < 0.001$) and 0.5 kg ha^{-1} mm^{-1} for precipitous slopes *TP* ($R^2 = 0.79$, $p < 0.001$). At the high grazing scenario, the slope of the regression line between phytomass and precipitation was 2.84 kg ha^{-1}

mm^{-1} for *TF* (R^2 = 0.86, p < 0.001), 1.0 kg ha^{-1} mm^{-1} of *TG* (R^2 = 0.60, p < 0.001) and 0.1 kg ha^{-1} mm^{-1} for *TP* (R^2 = 0.80, p < 0.001). The regression results indicate a decrease in productivity with increasing slope for both management scenarios.
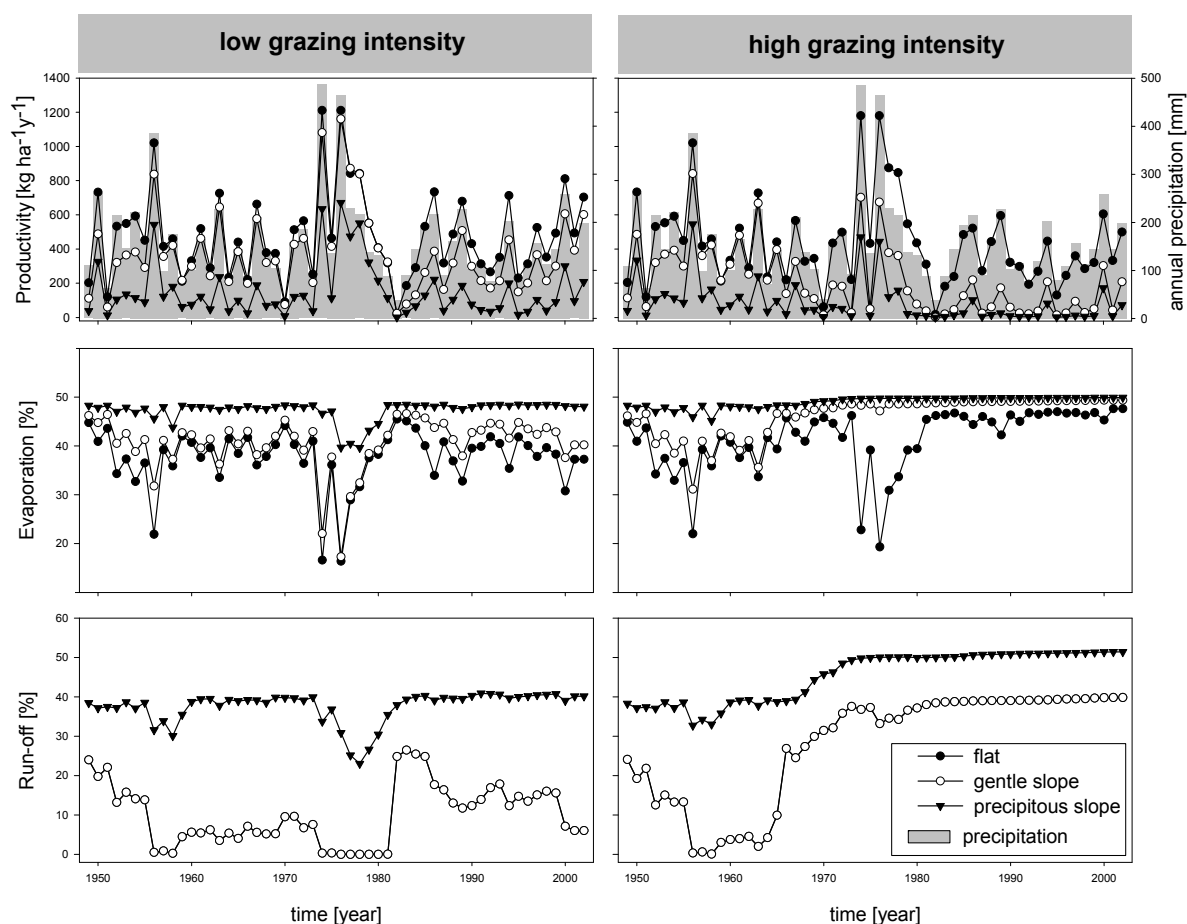
Figure 1: Time series of annual precipitation, total productivity and underlying hydrological processes (evaporation and run-off) for low (left) and high (right) grazing intensity. Medians of 500 simulation replicates are shown. Black circles represent plain scenarios, white cirles slope scenarios and triangles hill scenarios. Grey bars refer to annual precipitation.

The strong impact of slope, landuse option as well was the interplay of both factors (Figure 2) was evident while comparing the mean productivity of the last 40 years (multfactorial ANOVA, F = 187.55, p < 0.001). Topography and grazing had an over-riding effect on phytomass production over time, whereas slope affected productivity at both landuse scenarios differently with stronger impact under high grazing.

Hydrological processes - Annual run-off in the simulated years ranged from 0 to 50 % of annual precipitation (Figure 1). The range of annual evaporation in this time-span was 15 – 50 %. Both, annual run-off and evaporation were not affected by total phytomass in all scenarios. Annual run-
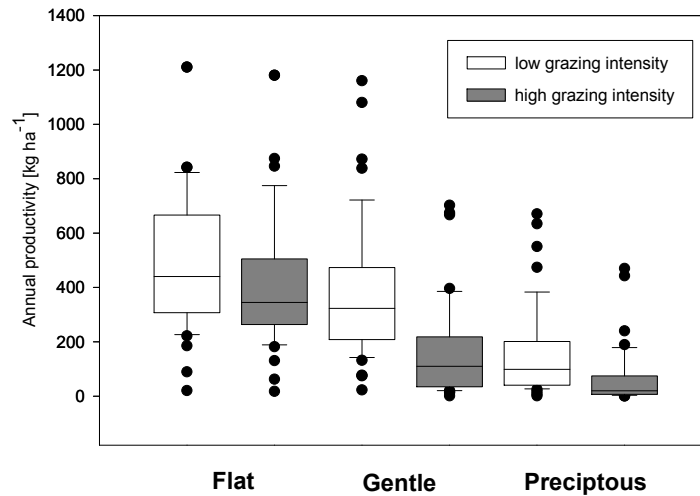
Figure 2: Simulated annual phytomass production (left axis) is strongly affected by topography and grazing. Labels on the x-axis refer to topographical scenario. Colour of boxplots refer to landuse (white: low grazing intensity; grey: high grazing intensity).

off and evaporation were regressed against total annual phytomass, slope and management method. We found a negative relationship between total annual phytomass and run-off with increasing slope for the low grazing (G_L) and the high grazing scenario (G_H). In areas with a 5% slope, *TG*, this negative relationship between total annual phytomass and annual run-off was low (G_L: $R^2 = 0.46$, p < 0.001; G_H: $R^2 = 0.04$, p < 0.001). In contrast, in areas with a 20 % slope, *TP*, we found no relationship between total annual phytomass and run-off at (G_L: $R^2 = 0.07$, p = 0.09; G_H: $R^2 = 0.04$, p = 0.23).

In flat areas (*TF*) evaporation from the soil was negatively affected by total annual phytomass (G_L: $R^2 = 0.86$, p < 0.001; G_H: $R^2 = 0.74$, p < 0.001). In contrast to Nabaos ($R^2 = 0.34$, p < 0.001), the negative relationship at the low grazing scenario between total annual phytomass and evaporation was confirmed for *TG* ($R^2 = 0.82$, p < 0.001). In areas where slope was 20% (*TP*) we found no relationship between annual phytomass and evaporation (G_L: $R^2 = 0.08$, p = 0.08; G_H: $R^2 = 0.04$, p = 0.22).

Vegetation composition - In all scenarios, vegetation composition was affected by landuse, slope and annual precipitation (Figure 3). At Gellap (high grazing impact), perennial grass shows highest mean proportion in total productivity in the flat area scenario *TF* and in the 5 % slope scenario *TG* (60 % vs. 58 %), followed by annual forbs (16 % vs. 19 %), shrubs (14 % vs. 13 %) and dwarf shrubs (10 % vs. 10 %). In contrast, in the 20% slope scenario *TP* the dominance of perennial grasses is shifted towards annuals and shrubs with values of 34 % for perennial grass, 31 % for annual forbs, 22 % for shrubs and 12 % for dwarf shrubs. At Nabaos mean proportion of perennial grasses (*TF* = 38 %; *TG* = 15 %; *TP* = 8 %) and dwarf shrubs (*TF* = 7 %; *TG* = 4 %; *TP* = 2 %) in
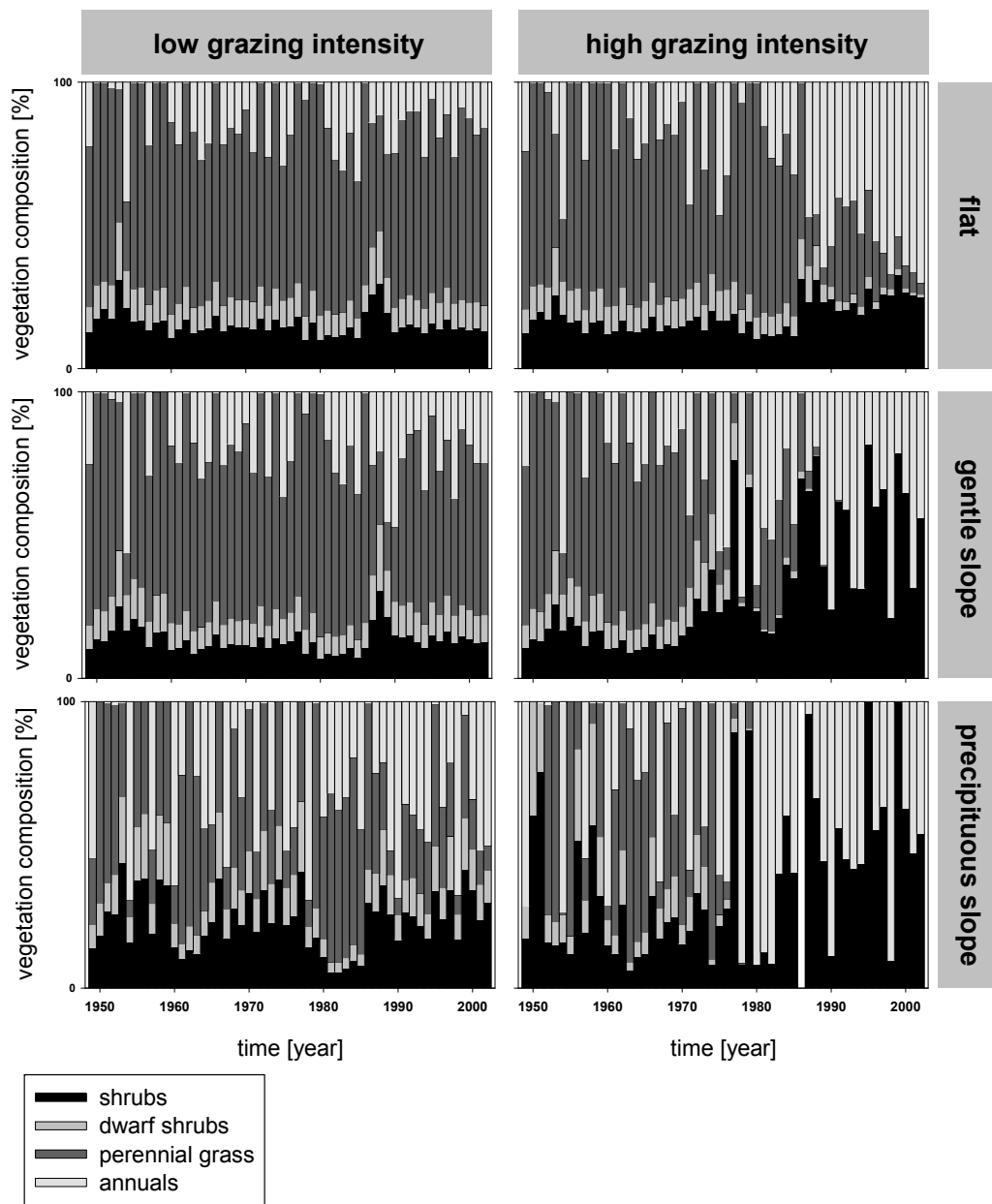
Figure 3: Time series of vegetation composition (left axis) is affected by slope, grazing and precipitation. Columns refer to different management scenarios (left: Gellap; right: Nabaos). Rows refer to scenarios without topography (top), slope scenarios (middle) hill scenarios (below). Propotion of perennial grass (dark grey bars) as well as dwarf shrubs (light grey bars) of total productivity decrease with increasing slope angle as well as grazing pressure and dominance is shifted towards shrubs (black bars) and annuals (white bars).

total show lower values. Their mean abundance decreases for the benefit of annual herbs (*TF* = 35 %; *TG* = 39 %; *TP* = 44 %) and shrubs (*TF* = 20 %; *TG* = 43 %; *TP* = 46 %).

Water use efficiency (WUE) **-** Mean *WUE* was negatively affected by slope angle at both management scenarios (Figure 4) with higher values at the Gellap than at the Nabaos scenario. Optimum *WUE* of 3.1 at Gellap and 2.5 at Nabaos were achieved at 0 % slope. At the Gellap scenario,

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WUE decreases nearly linearly with increasing slope and reaches the minimum value of 0.7 at the slope of 30 %. In contrast, increasing slope at the Nabaos scenario shows lower impact besides at 2 % of slope where *WUE* drops down to 1.5. Here, the minimum value of 0.4 can be found at the slope of 30 %.
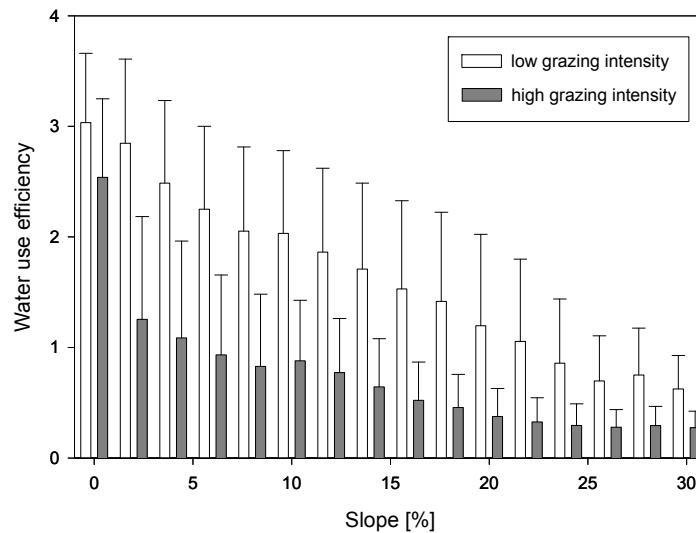

Figure 4: Effects of slope angle on water use effivciency at research sites with low (white bars) and high (grey bars) grazing intensity.

4.3. Sensitivity analysis

We conducted a series of sensitivity analyses to estimate the vulnerability of the model to uncertainties in parameter values and thus, to estimate the capabilities of the model. As the number of parameters is too high to display the impact of each parameter, we first grouped the parameters based on the simulated process they contribute to. Sensitivity of these parameter groups is given in Figure 5.

At the level of all processes, the model displayed higher sensitivities at Nabaos than at Gellap. Moreover, Nabaos, in contrast to Gellap, was most sensitive to parameters determining the mortality of vegetation types (*M*). Here, high stocking rates and continuous grazing affect survival of plants, vegetation cover, biomass and finally *WUE* . Sustainable management at Gellap mitigates
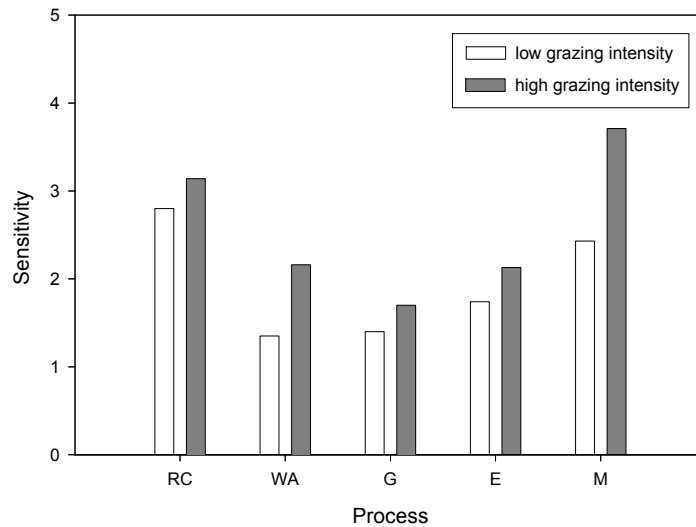
Figure 5: Sensitivity of the parameter groups at research sites with low (black bars) and high (grey bars) grazing intensity. Parameter are grouped based on the processes resource conservation (*RC*), water availability (*WA*), growth (*G*), establishment (*E*) and mortality (*M*). See text on Sensitivity Analysis for further description.

lated to grazing intensity. Comparing the residual parameter groups for both scenarios indicates high sensitivities for parameters concerning the impact of vegetation on the conservation of soil water (*RC*). This demonstrates the influence and importance of positive feedback mechanisms between vegetation dynamics and hydrological processes. The model was only little sensitive to parameter groups for growth (*G*), establishment (*E*) and remaining parameters determining water availability (*WA*).

5. Discussion

A major goal of our study was to assess the impact of topography on vegetation dynamics under two exemplary landuse managements (high versus low grazing impact). We found that productivity is strongly affected by topography, but the severity and temporal pattern of productivity yet depends on precipitation and management. Slope affects hydrological processes and associated productivity under different landuse options differently. Decreasing water use efficiency (*WUE*) with increasing slope at both landuse scenarios is consistent with the importance of water loss through run-off, resulting decreases in vegetation cover and increased evaporation. At little slope, low stocking rates (Gellap) maintain undisturbed vegetation, low values of run-off and evaporation. The resource conserving service of the landscape remains intact and productivity as well as *WUE* is comparable to the productivity of flat landscapes. Nevertheless, at steeper slopes water retention potential decreases leading to lower productivity as well as *WUE* and higher levels of run-off and evaporation. In contrast, overgrazing (Nabaos) reduces vegetation cover, production and WUE

whereas the landscape becomes less efficient at trapping run-off, leading to high losses of water even in landscapes with less steeper slopes.

This general process has been observed in other semi-arid and arid ecosystems. In these environments, a positive-feedback or self-reinforcing mechanism links water and vegetation (Cammeraat and Imeson 1999, Ludwig et al. 2000). Topography and spatial distribution of vegetation causes areas of runoff and run-on which lead to the development of islands of hydrologically enhanced biotic productivity (Ludwig 2005). In these 'resource conserving' drylands the concentration of resources increases the efficiency of their use and allows for higher net primary production (Noy-Meir 1973, Wilcox et al. 2003). For example, when water from bare patches accumulates in vegetated patches, it is stored at greater depths and is less subject to evaporation, i.e. more water is available to plants. If grazing alters the spatial and temporal relationships among these properties, the system will become leaky or non-conserving – less efficient at trapping runoff, leading to a loss of water. A positive feedback reinforces the degradation process, as higher run-off means less water available to plants (Davenport et al. 1998), including lower productivity, seedling establishment and germination rates as well as higher mortality (Montana 1992, Seghieri and Galle 1999). Finally, evaporation of soil water increases due to low levels of plant cover and resulting harsh thermal regimes with high temperatures (Domingo et al. 2000, Puigdefabregas 2005).

Moreover, we found that vegetation composition is affected by slope, grazing as well as precipitation, too. Abundance of perennial grass as well as dwarf shrubs decreases with increasing slope angle as well as grazing pressure and dominance is shifted towards shrubs and annuals. The relative value of the different vegetation types in semi-arid and arid rangelands is not only to provide forage production (provisioning ecosystem service), but also to regulate ecosystem processes, as in our case the conservation of the limiting resource water (regulating ecosystem service). The identification and quantification of ecosystem services of these vegetation types is important because many ecosystem services are not apparent to stakeholders or decision makers. Regulating services are particularly likely to be ignored, even though they are often crucial for the resilience of ecosystems and other ecosystem services (Carpenter and Folke 2006).

The importance of composition for productivity identified in recent studies (Hooper and Vitousek 1997, Tilman 1997) is based on the importance of soil water retention, determining plant production in semi-arid environments. The sensitivity of parameters concerning the impact of perennial vegetation on the conservation of soil water demonstrates the influence of positive feedback mechanisms between vegetation composition and hydrological processes.

The rapid erosion of ecosystem function, i.e. productivity, in simulated landscapes with distinct topography at high grazing intensities is due to preferential loss of perennial grass and dwarf shrubs. These vegetation types are most functionally important by facilitating or complementing

the functional properties of all other vegetation types by acting as a barrier to slow runoff and promote infiltration as well as reducing evaporation by shading. Disappearance of these vegetation types is associated with low soil water retention, establishment and growth opportunity. Establishment and biomass production of annuals is restricted to years of favourable precipitation. This shift in vegetation composition towards shrubs and annuals and associated loss of regulating service decreases provisioning ecosystem service, i.e. annual productivity and WUE.

Management based on ecosystem services requires a full understanding of the complex ways in which these services benefit humans (Farber et al. 2006). Understanding the impact of topography has strong implications for improving the management of semi-arid landscapes. In this study we could show that slope has strong impact on productivity and composition as run-off and vegetation growth was related. When grazing reduced vegetation cover, water loss due to increased run-off lead to an additional reduction in forage production and quality. Rapid losses in forage production can be avoided by using livestock management practices to maintain a good cover of perennial vegetation patches, particullary on rangelands with ascending slope.

6.   Appendix A

A.1   Water availability

Water availability (WP) is calculated for each vegetation type in each cell, influenced by rain, run-off, evaporation and competition (Figure A.1). These hydrological processes are based on cell-specific characteristics: soil texture (t), vegetation cover (v) and slope (s). The amount of the directly infiltrating rain equals annual rainfall (R) minus potential flowing water (R_f), and water input or discharge affected by run-off coefficient (r). Moreover, WP is reduced by evaporation (e_P), and competition coefficients (c_P):

$$W_P = \left(\left(R - R_f\right) + rR_f\right) * e_p * c_P \qquad\qquad \text{(A.1)}$$

RunOff – Run-off cannot be predicted from precipitation when aggregated annually (Wilcox et al. 2003). Thus, to calculate potential flowing water for the simulations (R_f) on an annual base, we analysed an hourly based rainfall set for the years 2001 -2003 (BIOTA-rainfall data). To estimate the average annual share of potential flowing water ($p = R_{f\,[data]} / R_{[data]} = 0.31$) for this area, the $R_{f[data]}$ was calculated for each of these years. Therefore, we summed up all potential run-off events, i.e. hourly rainfall events with rainfall intensity exceeding the mean infiltration rate of the landscape (depending only on the influence of soil texture and slope). For each simulated year R_f is then calculated by:

$$R_f = pR \qquad\qquad \text{(A.2)}$$

Within each simulated year, all grid cells are checked for run-off. r depends on the relation between water input (w_i) and infiltration rate (ir_C):

$$r = \frac{w_i}{ir_C} \qquad\qquad \text{(A.3)}$$

An iterative algorithm guarantees discharge flow-through. In each iterative step (i) r is updated as long as cells contribute and pass flow (Figure A.2). In the initial iterative step ($i = 1$) w_i equals the average potential run-off event, whereas ir_C is based on soil texture. Additionall, ir_C is positively affected by vegetation (v) and decreases linearly with increasing slope (s). For the estimation of water flow direction within the modelled cell grid, we adapted multiple flow direction methods (Tarboton 1997) which are used frequently in the analysis of DEM (Digital Elevation Model).
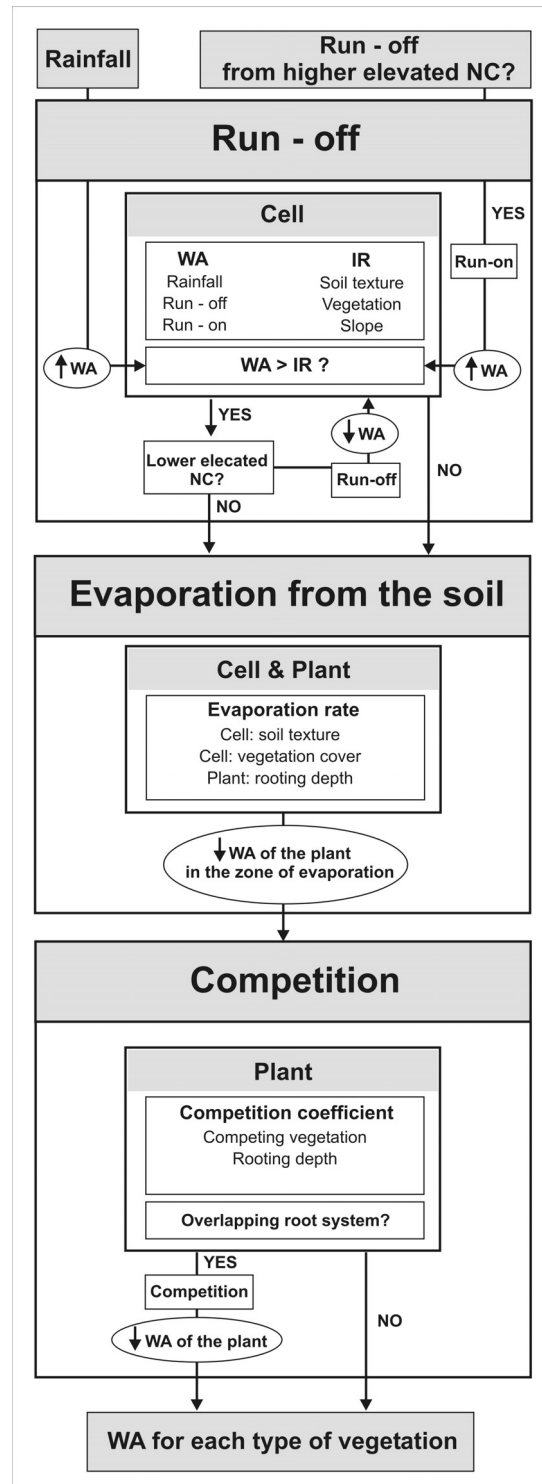
Figure A.1: Simplified flow-chart for the hierarchical calculation of water availability (*WA*). WA is calculated for each vegetation type in each cell. First, rainfall, run-off and run-on is estimated on the cell level. Run-Off is related to rainfall as well as run-on from neighbouring cells (*NC*) and calculated by the help of an iterative algorithm to guarantee discharge flow-through. Evaporation from the soil is related to cell attributes soil texture, vegetation cover and evaporative effect on vegetation types within a cell depends on their specific rooting depth. Finally, competition reduces water availability for vegetation types occupying the same soil horizon. Central boxes display hierarchical levels as well as attributes referring to the calculation of water availability. Squares mark processes and circles illustrate the outcome of these process. For more detailed description see text.

Thus, runoff source cells allocate water fractionally to each lower neighbor cell in proportion to the slope. In subsequent iterative steps, wi is equated to the input of all contributing cells and, as flow velocity increases with increasing distance to the source cell ir_C is updated by the cells slope ($ir_{C\_i} + 1 = ir_{C\_i} * s$).
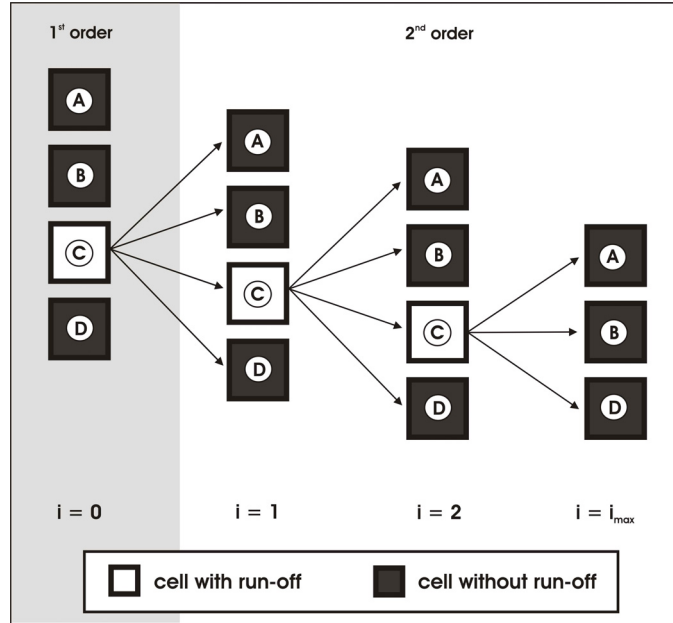
Figure A.2: Visualisation of the run-off rules as given in the text. Cells leading to run-off are marked white. In contrast, cells not able to produce run-off are marked dark grey. Grey bar marks 1st order runoff, white bar contains 2nd order run-off. i indicates iteration position and i_{max} represents the maximum number of iterative steps. Capital letters stand for runoff attributes: A) $RI_i/IR_i < 1$ and neighbour cell shows lower elevation B) $RI_i/IR_i < 1$ & neighbour cell shows higher elevation C) $RI_i/IR_i > 1$ and neighbour cell shows lower elevation D) $RI_i/IR_i > 1$ and neighbour cell shows higher elevation.

Evaporation – Due to evaporation from the soil, *WP* can be reduced up to a maximum evaporative effect (e_{max}) of 70% (LeHouerou 1984, Snyman 2000). This maximum evaporative effect (e_{max}) is related to a cells soil texture, positively influenced by vegetation *v*. Generally, deep rooting plants are able to access sources of soil water that extend below the zone of soil evaporation (Huxman et al. 2005). Here, evaporation is influenced by annual fraction of deep water infiltration (p_D) and vegetation type specific proportion of roots in the lower soil layer (R_L). We assume p_D to be positive correlated with water availability ($p_D = ((R - R_f) + rR_f) / R_{max}$). The evaporation coefficient (*e*) is calculated by:

$$e = e_{max} * \left(1 - \left(R_L * p_D\right)\right) * \left(1 - v\right)$$
(A.4)

Competition – Plant communities in low productive environments like arid and semi-arid areas are strongly influenced by competition (Huston and DeAngelis 1994, Callaway 1997). In cells with

overlapping root systems each vegetation type (v) has specific competitive effect on the particular vegetation types (c_P) (for description see impact of vegetation) by:

$$c_P = 1 - v \qquad (A.5)$$

We define vegetation types occupying the same niche to share soil moisture in an even way. In contrast, plants using soil moisture preferentially from the lower soil layer may be restricted in their growth and abundance by vegetation spreading their roots mainly in the upper layer. With respect to the ongoing discussion about root distribution we assume that herbaceous vegetation mainly refers to water in the upper soil layer. Woody vegetation is primarily supplied with moisture from deeper soil layers (Walter et al 1981), whereas dwarf shrubs shift their roots more to the upper soil layer (Schenk et al. 2002).

Table A.1: Impact of vegetation types on hydrological processes. Panels in the column headers refer to vegetation type. Pannels in the row headers refer to maximum strength of influence (P_{max}) of the respective vegetation type.

P_{max}	meaning	Shrub	Dwarf shrub	Perennial grass	annuals
v_{IR}	Increase of infiltration rate	4	5	6	-
v_{Evap}	Reduction of evaporation	30 %	50 %	100 %	-
R_L	Proportion of roots in the lower soil layer	20 %	50 %	75 %	100 %
S_C	Competitive effect on shrubs	100 %	70 %	80 %	-
DS_C	Competitive effect on dwarf shrubs	40 %	100 %	60 %	-
PG_C	Competitive effect on perennial grass	30 %	40 %	-	-
A_C	Competitive effect on annuals	30 %	40 %	100 %	-

Impact of vegetation - Within these hydrological processes, total influence of vegetation inside a cell (T_v) on water availability equals the influence of all vegetation types ($T_v = \sum I_p$). The impact of the respective growth types (I_P) is derived by a growth type specific maximum influence (I_{max}) governed by the proportion of its current (P_C) and maximum performance (P_{max}):

$$I_P = I_{max} * \frac{P_C}{P_{max}} \qquad \text{(A.6)}$$

Values for P_{max} for all vegetation types and processes are given in Table A.1.

A.2   Growth

Annual biomass production of herbaceous matrix vegetation, perennial grasses and annuals, (B_H) is related to particular annual water availability (W_H). For herbaceous vegetation, we use a growth coefficient (g = 3.04) derived from rainfall-grass production relationships of divers southern African savanna regions (Higgins 2000):

$$B_H = gW_H \qquad \text{(A.7)}$$

In contrast, annual biomass production of woody plant individuals (B_W) depends on the impact of water availability (w) and current height performance ($_h$) on maximum biomass production (B_{max}):

$$B_W = B_{max} * w * h \qquad \text{(A.8)}$$

where B_{max} differs with 1kg for shrubs and 0.2 kg for dwarf shrubs (Hoffman pers. com., Milton pers com). w equals 0 as long as water availability for the respective plant (W_P) falls below a lower threshold of 20 mm and increases linearly the more W_P matches a type-specific upper threshold in the need for water (W_{max}) (shrub = 500 mm; dwarf shrub = 200 mm). h shows lowest values if current height (H) is low and decreasing linearly the more it gets adjusted to maximum height (H_{max}) of a plant (shrub = 2m; dwarf shrub = 0.5m). Each year, H is updated by annual growth rate ($H_t = H_{t-1} + Ht * gr$). Annual growth rate (gr) is related to maximum growth rate (gr_{max}) of 10% (Scholes and Walker 1993), h and w by:

$$gr = gr_{max*} * \left(1 - \frac{1}{h}\right) * w \qquad \text{(A.9)}$$

A.3   Grazing

The model simulates spatial homogeneous grazing and browsing on herbaceous and woody vegetation. Vegetation types differ in their palatability for grazers and browsers. What and to which amount a plants biomass will be consumed depends on the relation of available (B_A) and needed forage (B_N) as well as its specific palatability. For each woody and matrix plant the biomass is reduced by the proportion of biomass extraction (p_e):

$$p_e = \frac{B_N}{B_A} \tag{A.10}$$

To calculate pe, the landscapes available biomass is added up and classified in terms of palatability (low, high) for grazers (B_{AG}) as well as browsers (B_{AB}).

$$B_A = B_{AGHigh} + B_{AGLow} + B_{ABHigh} + B_{ABLow} \tag{A.11}$$

In turn, BN is subdivided in needed biomass for grazing (B_{NG}) and browsing (B_{NB}). The calculation of B_{NG} (first term of A.13) and B_{NB} (second term of A.13) is based on the types of livestock and their annual stocking rate (s), as each type of livestock is attributed with a specific share of grazing (s_G) and browsing (s_B) in annual intake (I_a):

$$B_N = I_a * s(s_G + s_B) \tag{A.12}$$

A.4   Establishment

In arid and semi-arid environments sufficient moisture (e.g. O'Connor 1996) and the occurrence of seeds (e.g. Milton 1994) are the main conditions for successful establishment. Furthermore, little food for livestock heightens trampling effects and the probability that livestock feeds on the seedlings (Danckwerts anf Stuart-Hill 1988, Milton 1994, Carrick 2003). So, the cells probability of successful establishment (P_E) for the perennial vegetation (woody plants and perennial grasses) is determined by cell-specific probabilities of seed (P_S) and water availability (P_W) as well as the probability to survive grazing (P_G):

$$P_E = P_S * P_W * P_G \tag{A.13}$$

To find out whether P_E of the perennial plants enables establishment it has to exceed a randomly drawn number between 0 and 1. In contrast to perennial grasses, seedling survival of woody vegetation in the first years after establishment is a rare event. Thus, cells are checked on establishment of mature plant individuals after the progress of 2 computed years. Meanwhile, P_E is influenced by annual negative effects of grazing and drought. Finally, annuals, producing large numbers of seeds and persistent seed banks (Jackson and Roy 1986, Veenendaal 1996) are restricted by water availability and grazing pressure but not by seed availability.

Seed availability - P_S for perennial plants is related to (i) annual seed production of the landscape (*Prod*), (ii) dispersal (*Disp*) and (iii) seed persistence (*Pers*).

$$P_S = \mathrm{Pr}od * Disp * Pers \tag{A.14}$$

(i) Year-to-year variation in seed production depends on abundance and performance of fertile individuals (Milton 1994). Consumption of flowers by livestock reduces seed output (O'Connor and Pickett 1992, O'Connor 1994). Consequently, *Prod* depends on the share of total biomass after grazing (B_{AG}) in maximum biomass (B_{Max}) at the landscape level. We assume that Prod equals highest values if B_{AG} exceeds 10% of B_{Max}:

$$\text{Pr}\,od = \frac{B_{AG}}{B_{Max} * 0.1}$$

(A.15)

(ii) The complexity of processes that move seeds is high: seeds can be found in cells with fertile parent plants ($F_C = 1$) and adjacent cells ($F_{NC} = 0.5$). Long-distance dispersal events are rare but biologically important (Higgins 1999). Small-seeded species produce higher numbers of seeds per plant in comparison to large-seeded species (Leishman et al. 2000). In consequence, they have better dispersal abilities (Okubo and Levin 1989), increasing their probability of seed occurrence independent to the distance of a fertile individual (P_{ldd}). We assumed P_{ldd} for perennial grasses being 1 and P_{ldd} for woody vegetation being 0.25. Thus, *Disp* of the individual cells is calculated by adding up all factors up to a maximum value of 1:

$$Disp = F_C + F_{NC} + P_{ldd}$$

(A.16)

(iii) Knowledge of seed banks in arid environments is sparse (Jones and Esler 2004). Resistance in the soil is associated with small seeds (Price and Joyner 1997) because small sized seeds can escape predation by quickly becoming incorporated into the soil (Skoglund 1992). Therfore, *Pers* equals the seed size-specific survival coefficient (s_P) of the previous years seed availability (PP_S):

$$Pers = PP_S * s_P$$

(A.17)

Therefore, in comparison to perennial grasses ($s_p = 0.4$), seed banks of large seeded savanna woody plants ($s_p = 0.2$) are not very long-lived.

Water availability - The occurrence of sufficient water to allow for germination and successful establishment beyond few months is a rare event (Wilson and Witkowski 1998, Esler 1999). During the first year, seedlings from large seeds are more tolerant of drought (Skoglund 1992, Moles and Westoby 2004). Hence, water availabilty (P_W) is not restricting the emergence of seedlings if a month exceeding the minimum water availability for germination (G_{Min}) of 30 mm (Wiegand and Milton 1996) is followed by a month exceeding the seed mass related minimum water availability for seedling survival (S_{Min}) with $S_{Min} = 15$ for herbaceous and $S_{Min} = 10$ for woody vegetation. Competitive effects of herbaceous vegetation influence strongly and can even prevent seedling

survival (Knoop and Walker 1985, Scholes and Archer 1997). So, P_W is reduced by the standing green biomass of a cells perennial gras (B_G) in relation to the maximum value ($MaxB_G$) up to 100%:

$$P_W = P_W * \left(1 - \frac{B_G}{MaxB_G} \right) \qquad (A.18)$$

Disturbance by grazing – Little food for livestock heightens trampling effects and the probability that livestock feeds on the seedlings. Therefore, the probability of seedlings to survive grazing (P_G) is related to livestocks' needed (B_N) and available biomass (B_A):

$$P_G = 1 - \left(\frac{B_N}{B_A} \right) \qquad (A.19)$$

A.5 Mortality

Survival of perennial plants is environmentally determined by the availability of water (Milton et al. 1995, Fensham and Holman 1999, Milton and Dean 2000) and the impact of grazing by livestock (O'Connor 1994). We related the probability to die off to a basic mortality (*mort*) of 0.01 for perennial grass and woody plants. High probability to die off (*mort* = 0.6) appears in subsequent years (Y_D) of disturbance by drought or overgrazing if productivity is extremely reduced (Milton and Dean 2000). Due to better physiological adaptation, woody plants ($Y_D = 5$) show higher disturbance tolerance than perennial grasses ($Y_D = 3$). Plants survive if mort falls below a randomly drawn number between 0 and 1.

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8. Link to the proceeding chapter

In the first chapter, I investigated the impact of topography on vegetation dynamics at the hillslope scale under two exemplary landuse managements. I showed that the sensitivity of small scale soil-plant interactions to topography is strongly affected by disturbances like overgrazing. However, decisions for the conservation of biodiversity and sustainable management of natural resources demand an understanding of ecological processes at the landscape scale.

In the following chapter, I will present a modelling approach that has the power to transfer and integrate information between spatial scales. I combined spatially explicit modelling with remotely sensed data and GIS for initialisation and parametrisation of the landscape model. Moreover, I will investigate the importance of spatial exchange of water at the landscape scale for the resilience of rangelands in semi-arid and arid regions with distinct topography.

4 Scaling up ecohydrological processes - the role of source-sink systems in water limited environments [1]

1. Abstract

In ecology, best understanding of processes and patterns happens at fine scales. In contrast, decisions for the conservation of biodiversity and sustainable management of natural resources demand an understanding of ecological processes over long-time periods and at broad scales. These difficulties are further exacerbated when spatial interactions produce large responses that overwhelm local effects. In this study, we present two grid based simulation models which have the power to transfer and integrate existing information between spatial scales. One version includes spatial exchange of water among the grid cells wheras the other version disregards spatial interaction. We combined technologies of remote sensing, GIS and stochastic modelling to adress landcover change in arid landscapes. Using transition probabilities derived from a small scaled simulation model, we successfully reproduced vegetation dynamics, composition and productivity as well as hydrological processes. We applied both landscape models to the situation of a sustainable used research farm and communally used and degraded farming land in semi-arid Namibia. Model results could successfully be compared with historical, remotely sensed estimates of total biomass production (I-NDVI) for 1981-2001. Our simulation experiments show that spatial interaction by exchanging water among vegetation patches increases biomass production at light grazing intensities. In contrast, overgrazing destabilizes positive feedbacks through vegetation and hydrology and decreases the number of hydrological sinks. The buffer capacity of these hydrologicaly sinks disappears and run-off inreases. Spatial interactions cause downstream out of the simulated system and artificial droughts occur even in years with good precipitation.

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[1] A version of this chapter has been submitted to *Ecosystems* as: A. Popp, M. Vogel, N. Blaum, F. Jeltsch: Scaling up ecohydrological processes - the role of source-sink systems in water limited environments

2.   Introduction

Decisions for the conservation of biodiversity and sustainable management of natural resources are made for long time periods and at large spatial scales (Peters et al. 1997, Miller et al. 2004). In contrast, our understanding of the underlying ecological processes e.g. local water availability triggering germination rates and plant growth is high at small spatial and temporal scales because most empirical data are collected for small areas and over a short duration (Levin 1992, Rastetter et al. 2003). Therefore, the knowledge from short-term and small scale studies needs to be projected to regional and global scales that are relevant for decision making (Wessman 1992).

However, extrapolation of information across scales provides difficulties as we do not know to which extent spatial interactions, like the movement of surface water by run-off in water limited environments, affect ecosystem dynamics at large scales (Levin 1992, Wootoon 2000, Strayer 2003, Urban 2005). Omission of these processes may directly affect the accuracy of predictions (Heuvelink 1998, Weaver and Perera 2004). Run-off occurs at multiple spatial scales if rainfall intensity exceeds soil infiltration capacity (Rango et al. 2006). Local differences in infiltration capacity are induced by topography, soil texture and positive feedback mechanisms between water and vegetation (Wilcox et al. 2003).

Many arid landscapes are source-sink systems, where plant productivity is determined by surface run-off from bare areas to vegetated patches. Therefore, theoretical (Noy-Meir 1973, Scheffer et al. 2001, Ludwig et al. 2005, Urban 2005, Peters and Havstad 2006) and model investigations (van de Koppel et al. 2002, van de Koppel and Rietkerk 2004) suggest that spatial re-distribution of rainfall by run-off increases productivity and resilience of arid ecosystems.

Disturbances like grazing can disrupt this fundamental process by changing vegetation structure and composition (e.g. Ludwig et al. 1997). The system may loose its buffer capacity and become less efficient at trapping runoff, leading to a loss of water. Maintaining so called 'resource conserving' drylands (Wilcox et al. 2003) may have profound implications for management of semi-arid and arid rangelands.

In the past, spatial transition based models like Markov chains have often been used to explore vegetation dynamics over long time periods and on large scales (e.g. Baker 1989, Turner 1989, Avecado et al. 1995, Baltzer 2000, Logfoet and Lesnaya 2000, Urban 2005). They are based on stochastic processes and can be parameterised by estimating transition probabilities between discrete states of the observed system. Most previous studies utilized data sampled from field surveys, existing maps, aerial photographies or satellite imageries to estimate transition probabilities (e.g. Muller and Middleton 1994, Brown et al. 2000, Jenerette 2001, Weng 2002). Uncertainty in these studies remains relatively high because spatial interactions like the movement of surface water by

run-off are not considered and data is limited, i.e. the transition probabilities are often derived from short-term data with no mechanistic description of processes (Baker 1989, Tucker and Anand 2005, Urban 2005).

To investigate the impact of (i) spatial interactions and (ii) disturbance on large-scale vegetation dynamics in arid rangelands we implemented two variants of a stochastic and spatially explicit landscape model on the basis of Markovian modelling that simulates annual biomass production of a dwarf shrub savannah with distinct topography in arid southern Namibia (Karas Region). One version simulates lateral exchange of surface water, whereas explicit consideration of spatial interaction is eliminated in the second version. We used a site-specific simulation model, operating at small scales (*TOPMAN*, TOPographical MANagement), to derive data and information which is handed over to the landscape model. This mechanistic approach guarantees that data collected and processes estimated at smaller scales are included in our application. Elevation of the landscape's grid cells is parameterised by remotely sensed digital elevation models (DEM). We compute annual productivity of the four most abundant vegetation types for two contrasting management methods which are adapted to a sustainable used research farm and a communal farming land, on which grazing pressure is not controlled. Finally, we compare simulated annual biomass production with remotely sensed estimates of annual biomass production (NDVI: Normalized Difference vegetation Index) for the years 1985 to 2000.

3. Material and Methods

3.1. Study area

The study area is located in the Nama Karoo, southern Namibia. Vegetation cover and productivity are low and depend on erratic and highly variable rainfall (annual mean: 150 mm). The main topografical features of the study area are flat regions, as well as regions with gentle and precipitous slopes (Kuiper and Meadows 2002). Perennial grasses (e.g. *Stipagrostis uniplumis*) dominate the herbaceous vegetation if the rangeland is in good condition but are replaced by annual grasses (such as *Schmidtia kalahariensis*) and unpalatable shrubs like *Rhigozum trichtomotum* when rangeland is heavily utilised (Kuiper and Meadows 2002). Most important type of land use in the communal area (Nabaos) and the Research Station (Gellap) is small stock farming. Gellap has 160 purposely under-stocked camps (0.05 SSU – small stock unit), where animals graze in rotational system. Resting periods of camps (without grazing) of at least one year prevent overgrazing (Kuiper and Meadows 2002). In contrast, the communal farming land is managed under a communal land tenure system wherein livestock movement in the area is not controlled and overstocking (0.2 SSU) has strong impact on the rangeland resource.

3.2.   Landscape model

The grid based landscape model simulates vegetation dynamics and interlinked hydrological processes of a dwarf shrub savannah with distinct topography in arid southern Namibia. Data on these dynamics and processes are derived from a small-scale (spatial resolution: 3x3m cells, 33 x 33 cells = 1 ha) and spatially explicit simulation model (TOPMAN, for more details see chapter 1). The area simulated by the small scale model (1 ha) was used as spatial resolution (cell size) for the landscape model. Each cell is specified by its position within the grid, elevation, water availability, vegetation composition and productivity. Dynamics of the simulated vegetation types (perennial grass, annual forbs, dwarf shrubs and shrubs) on the cell level are based on the concept of State-and-transition models (Westoby et al. 1989). These models provide a relatively simple, management-oriented way to classify land condition (state) and to analyse the impact of factors that might cause a shift to another state (transition). The stochastic process of State-and-transition models and resulting forecasting of land cover change can be projected by Markov chain models (Markov 1907). To construct a Markov chain, we first identified vegetation states for the research area jointly with Namibian rangeland experts like farmers and extension officers. Definition of these six states is related to the percentage coverage of shrubs and perennial grass (Table 1).

Table 1: Definition of vegetation states for the research area. Panels in the column headers refer to cover (%) of the respective vegetation type (PG = perennial grass; W = woody vegetation). Pannels in the row headers refer Vegetation State, enumerated by one to six.

	$Cover_{PG}$ (%)	$Cover_W$ (%)
State 1	30 – 100	40 – 100
State 2	0 – 29	40 – 100
State 3	50 – 100	0 – 40
State 4	10 – 49	0 – 40
State 5	0 – 9	10 – 40
State 6	0 – 9	0 – 9

Afterwards, we calculated annual transition probabilities between these states from simulations of the small scale model *TOPMAN* for different classes of slope, water availability and land use. For slope, we defined four classes: flat (<6%), gentle (6-10%), steep (11-1%) and precipitous (>15%).

Water availability was classified in four categories of annual rainfall (Figure 1): 1=poor (<100mm), 2=moderate (100-139mm), 3=good (140–179mm) and 4=very good (>180mm).
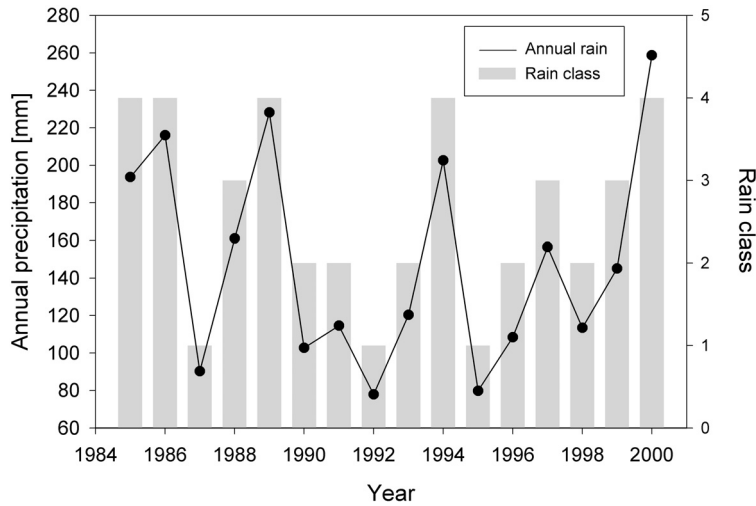
Figure 1: Time series of annual precipitation and rain class. Annual precipitation (left axis) and its subdivision into rain class (right axis). Water availability of a given year was categorized as poor (1), moderate (2), good (3) and very good (4).

Within each time step (1 year), the landscape model calculates the following modules in the given order: water availability, vegetation dynamics and productivity (Figure 2). Each model is explained below.

3.2.1. Model Initialisation

Calculation of the slope (s) of each 1 ha cell is based on elevation (e_c) and side lenght (l = 100 m) of the respective cell and elevation of the neighbouring cells (e_{nc}):

$$s = \frac{e_C - e_{NC}}{l}$$

(1)

Elevation was initialised with a digital elevation model (DEM), derived by remote sensing based radar data. The raster DEM is processed interferometrically from SRTM-C-Band data (Jensen 2000) with an original spatial resolution of 88m x 88m in x and y direction and 1 m resolution of the altitude (z direction). The data have been preprocessed, applying a 3 x 3 kernel low pass filter to reduce radar system inherent errors, caused by signal noise ("salt-and-pepper-effect"), and shadow effects (Lewis 1976). Application of this filter leads to a smoothening of high contrast image areas. To fit the 100m x 100m cell size of the landscape model, the DEM subset of the study area has been resampled, using a Nearest Neighbour algorithm.
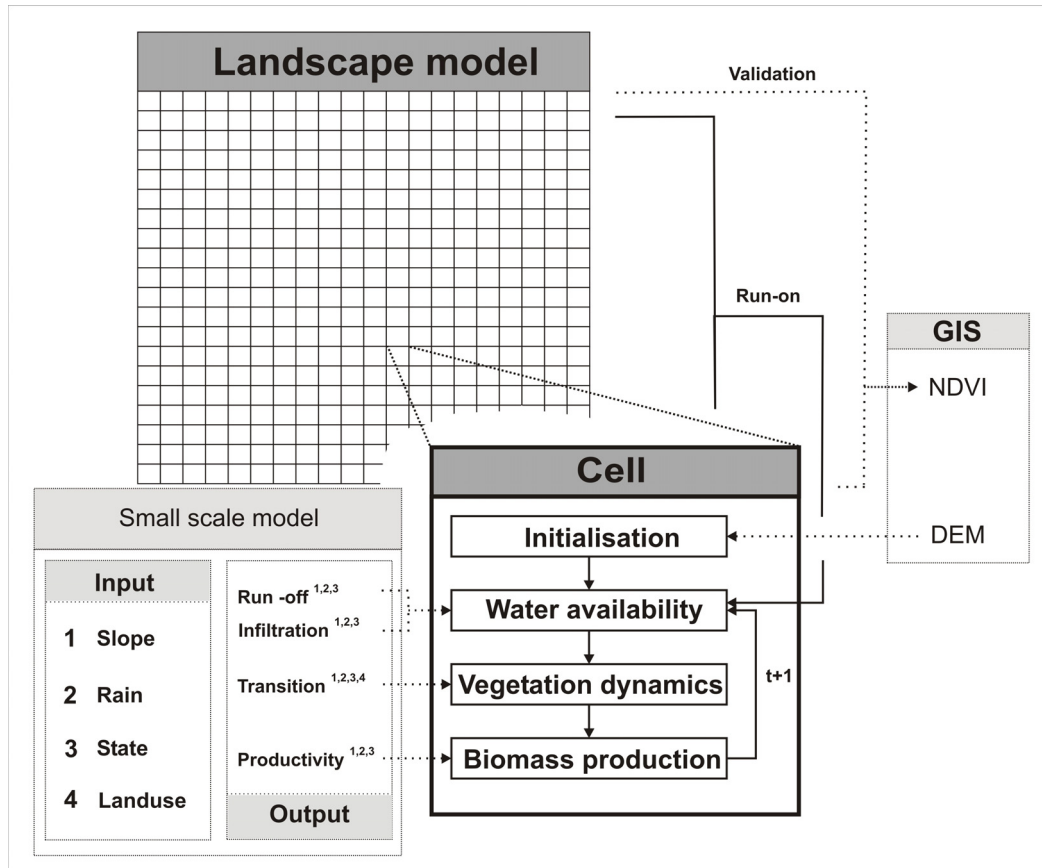
Figure 2: Visualisation of mechanistic upscaling approach and simplified flow chart. We used a small-scale simulation model to derive data for vegetation dynamics, productivity and linked hydrological processes of the alandscape model. Elevation of the landscape's grid cells is initialised by remotely sensed digital elevation models (DEM). For validation, simulated annual biomass production is compared with remotely sensed estimates of annual biomass production (NDVI). Solid lines represent processes within the landscape model (flow chart). Dashed lines illustrate data flow between different disciplines and scales. Numbers refer to basic attributes of the small-scale model (Input) affecting transferred data for the landscape model (Output).

For initialisation of the vegetation we used the vegetation structure of an undisturbed dwarf shrub savanna. Since little is known about this vegetation structure we assumed an undisturbed coexistence of perennial grasses and woody vegetation. Thus initial vegetation condition for each cell was set to state 3.

3.2.2. Vegetation Dynamics

We used a state and transition approach to simulate the vegetation dynamics. Transition probabilities between the vegetation states were calculated as Markovian stochastic processes (Markov 1907): a state at time t depends on the state at time $t-1$ and the impact of exogenous factors water availability, slope and present landuse. A $m \, x \, m$ transition matrix (P) contains the conditional probabilities p_{ij} that a cell in state i at time t will transition to state j at time $t+1$. For m states P has the form:

$$P = \begin{bmatrix} p_{11} & p_{12} & \cdots & p_{1m} \\ p_{21} & p_{22} & \cdots & p_{2m} \\ \cdots & \cdots & \cdots & \cdots \\ p_{m1} & p_{m2} & \cdots & p_{mm} \end{bmatrix} \tag{2}$$

P is row-standardized, such that the sum of transition probabilities from a given state is always equal to one:

$$\sum_{j=1}^{m} p_{ij} = 1 \quad i = 1, 2,\ldots, m \tag{3}$$

The states $p(t)$ at time t can be calculated by:

$$p(t) = p(t-1) \cdot P \tag{4}$$

We derived transition probabilities by calculating transition probabilities of the process based small-scale simulation model. Maximum likelihood estimates of the transition probabilities (Anderson and Goodman 1957) are then:

$$p_{ij} = \frac{n_{ij}}{\sum_{j=1}^{n} n_{ij}} \tag{5}$$

Where n_{ij} is the simulated number of transitions from state i to state j. To gain these values we run the small-scale model for 100 years with 500 repetitions.

Generally, we assume that (i) transition probabilities are constant over time and (ii) transitions are spatially independent. An approach to model nonstationarity is to switch between different stationary matrices (Rejmanek et al. 1987). Thus, to consider variability in space and time of transition probabilities related to water availability, slope and land use option we generated transition matrices for all combinations of these exogenous factors.

3.2.3. Productivity

Annual phytomass production of the four vegetation types is dependent on the cells slope, present vegetation state and water availability. For each vegetation type we calculated productivity coefficients from multiple linear regressions of biomass on slope, vegetation state and water availability simulated by the small scale model.

3.2.4. Water availability

We implemented two versions of the landscape model. One version disregards lateral exchange of surface water, whereas explicit consideration of spatial interaction is considered in the other. In the first version, water availability (W_C) is contingent on annual precipitation (p_C). In the case of spatial interaction (second version), W_C is not only related to annual precipitation (p) but also to run-on (r_C) from neighbouring cells and can be expressed by:

$$W_c = p + r_c \tag{6}$$

p is homogeneous for all cells, whereas r_C is based on a cell specific capacity to absorb run-on (ir_C) and the contribution by run-off from neighbouring cells (r_{NC}):

$$r_C = r_{NC} - ir_C \tag{7}$$

We used an iterative algorithm to calculate surface water flow for each simulated year: in the first step, each cell's $ir_{C,0}$ and $r_{NC,0}$, calculated by the small-scale model, are based on rain class as well as a cell's slope class and current vegetation state.

In each following iterative step $r_{NC,i}$ is updated until infiltration of a cell is saturated ($ir_{C,i} = 0$) and until no more cells pass flow ($r_{NC,i} = 0$). For the next iterative step $ir_{C,i+1}$ is actualised by:

$$ir_{C,i+1} = ir_{C,i} - r_{C,i} \tag{8}$$

We used multiple flow direction methods to estimate surface water flow directions across cells (Quinn et al. 1991, Tarboton 1997). Thus, cells with run-off allocate water fractionally to each lower neighbour cell in proportion to the respective slope.

3.3. Small-scale simulation model

Transition probabilities and phytpmass production are derived from a small scale simulation model. In the following we give an overview of the numerous parameters and processes included. A detailed model description has been presented in chapter 1.

The spatially-explicit and individual based model simulates the vegetation dynamics of a 1 ha area (100 x 100 m, 33 x 33 cells). Cell size is 3 m x 3 m, that corresponds to the maximum observed diameter of a shrub. Herbaceous vegetation (perennial grass and annuals) are treated as matrix plants, and a cell is either occupied or not. Woody plants are simulated individually and each cell contains a list of plant individuals. Slope angle is included by decreasing elevation values of the cells towards one side of the landscape. For each cell, water availability, establishment, phytomass production, grazing and mortality are simulated in annual time steps

Water availability - Cell-specific water availability of the different vegetation types is influenced by rain, run-off, evaporation and competition. Run-off occurs as infiltration-excess overland flow from high elevations to low-levelled areas, controlled by infiltration characteristics. Infiltration rates are related to the cells soil texture, vegetation cover and slope. Moreover, soil texture and vegetation cover have an impact on evaporation reducing soil water content in the upper soil layer. Competitive effects of vegetation reduce the water availability for establishment and, in cells with overlapping root systems, vegetation has a competitive effect on the neighbouring vegetation types.

Establishment - The cells' probability of successful establishment for the vegetation is determined by site-specific probabilities of seed and water availability as well as the probability to survive grazing.

Growth - Biomass production of the herbaceous vegetation is related to a rainfall-grass production relationships of divers southern African savanna regions (Higgins, 2000). In contrast, annual biomass production of woody plant individuals depends on impacts of water availability and current height performance.

Grazing - The small scale model simulates grazing and browsing on herbaceous and woody vegetation. Vegetation types differ in their palatability for grazers and browsers. What and to which amount a plants biomass will be consumed depends on the relation of available and needed forage as well as its specific palatability.

Mortality - Survival of perennial plants is environmentally determined by the availability of water and the impact of grazing by livestock (O'Connor, 1994; Milton and Dean, 2000). Here, the probability to survive is related to the plants performance, since disturbances as drought or overgrazing have strong influence on productivity. Within the group of perennial plants differences among species in disturbance tolerance results in better physiological adaptations to disturbance.

3.4. Simulation analysis

We used the landscape model to simulate vegetation dynamics and productivity of perennial grass, annuals, dwarf shrubs and shrubs for 150 years. Effects of connectivity and spatial explicity of overland flow on dynamics and productivity of the most abundant vegetation types was assessed for a purposely under-stocked and rotationally grazed research farm (Gellap) and a communal and overstocked farming land (Nabaos). For model analysis, we used the years 1985 to 2000 as remotely sensed data is available only for this time period and initialisation effects could be excluded. Due to the stochastic processes in the model, no single run is representative. Therefore, we started 50 repeats for each model type and scenario.

3.5. Model validation

In arid and semi-arid landscapes, remotely sensed Normalized Difference vegetation Index (NDVI) is strongly correlated with phytomass production (e.g. Tucker et al. 1986, Prince and Goward 1996, Yang and Prince 2000, Wessels et al. 2006). For model validation, we therefore compared simulation results of annual phytomass production for both study sites (low grazing impact versus high grazing impact) with remotely sensed estimates of annual phytomass production (I-NDVI).

NDVI is calculated from the red and near-infrared channels from optical remote sensing imagery (Tucker and Choudhury 1987):

$$NDVI = \frac{NIR - R}{NIR + R} \qquad (8)$$

where NIR is the reflectance in the near infrared band and R the reflectences in the red band. Temporal traces of NDVI from 1985 to 2001 were obtained from NOAA/NASA Pathfinder Land data archive (PAL).

I-NDVI was calculated for each sampling-domain from seasonal summations (October to Septemper) of differences between NDVI and minimum NDVI from the seasons 1985/86 to 2000/01 (Holm et al. 2003). Reference values of I-NDVI have been calculated for both study sites over an area of 8km^2 each.

4. Results

4.1. Exclusion of spatial interaction (non-spatial model)

Annual total phytomass - Annual total phytomass of all simulations ranged from 79 t per ha at high grazing intensity (Nabaos) in 1992 to 475 t per ha at low grazing intensity (Gellap) in 2000 (Figure 3). Averaged over the timespan of 15 years total phytomass production at the scenario with low grazing intensity exceeds total phytomass production at the scenario with high grazing intensity 1.32-fold. Linear regression analysis indicated that total phytomass simulations at the scenario with low grazing intensity ($R^2 = 0.97$, $p < 0.001$) and the scenario with high grazing intensity ($R^2 = 0.99$, $p < 0.001$) increased with annual precipitation.

Productivity of vegetation types – Figure 4 reveals largest share in mean total productivity for annuals (45 %), followed by perennial grass (31 %), shrubs (18 %) and dwarf shrubs (6 %) for the scenario with low grazing intensity. At the scenario with high grazing intensity, the proportion in mean annual total productivity was clearly decreased for perennial grasses (19 %) as well as dwarf shrubs (3 %) and dominance was shifted towards annuals (57 %) and shrubs (22 %).
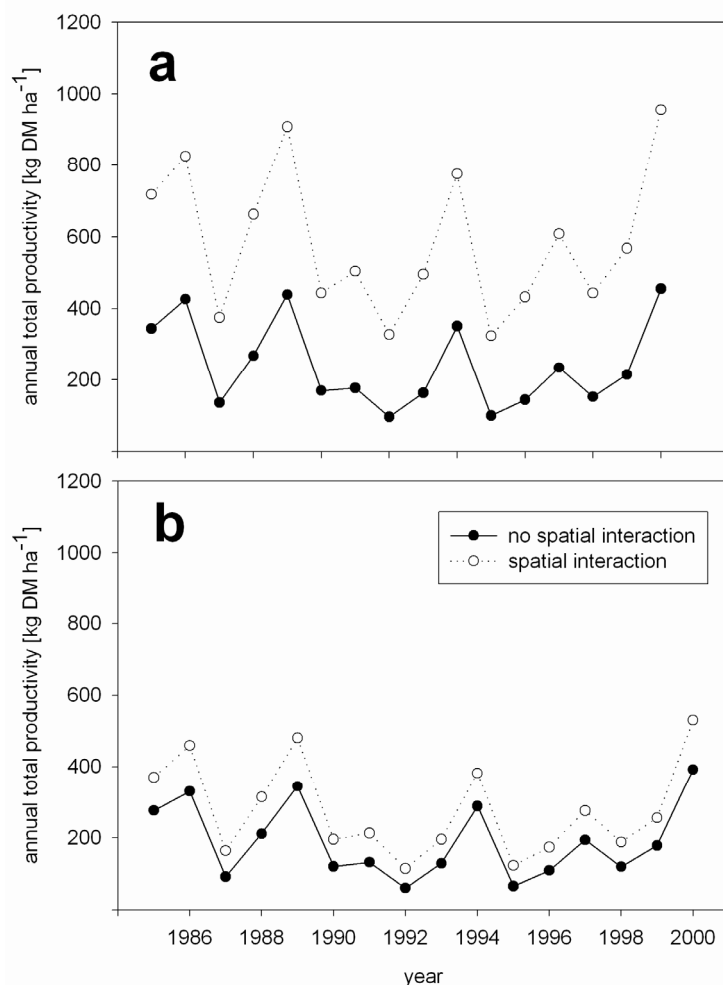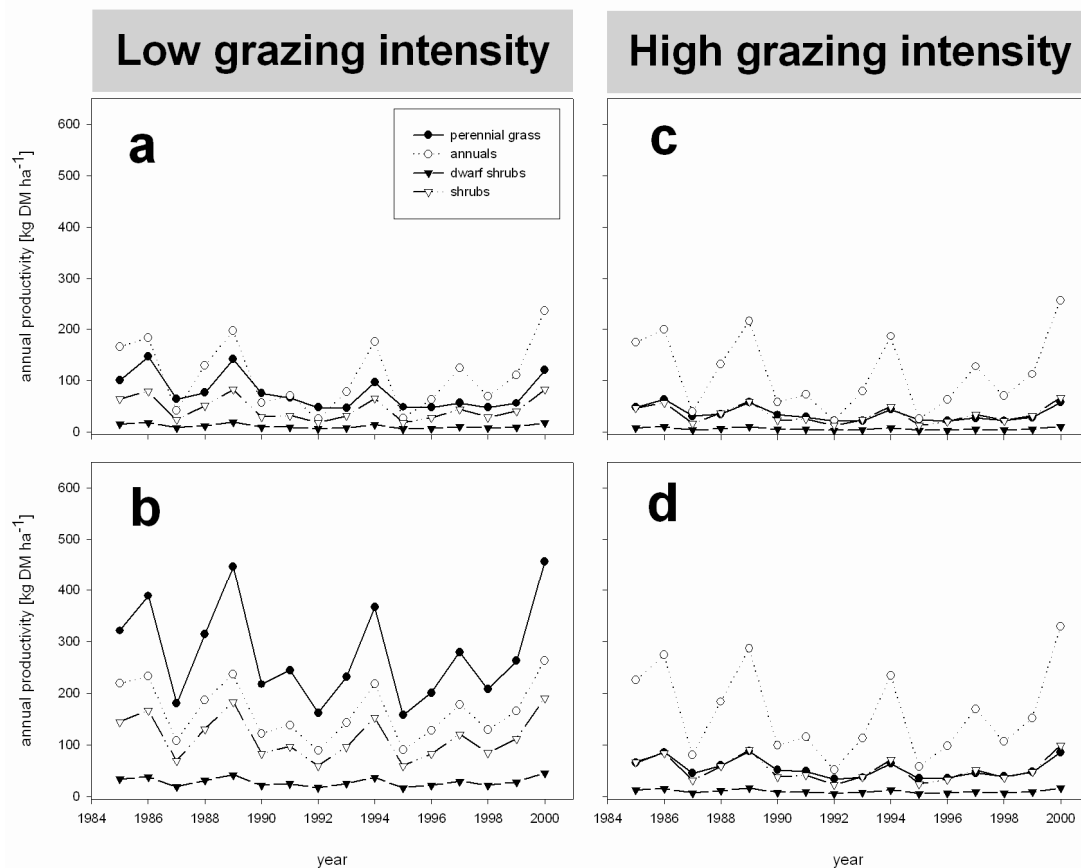
Figure 3: Time series of annual total productivity. Medians of 500 simulation replicates are shown. Annual total productivity at (a) low grazing intensity (Gellap) is strongly affected by spatial interaction. Low impact of spatial interaction can be found at the scenario with high grazing intensity (Nabaos) (b). Black circles represent scenarios without spatial interaction, and white cirles scenarios with spatial interaction.

Vegetation state composition - Productivity of the vegetation types is based on vegetation states of the cells. In comparison to the scenario with low grazing intensity, overgrazing at the scenario with high grazing intensity decreases the mean number of cells for the years 1985 to 2000 (NC) in state 1, 2, 3 and 4 and leads to dominance of state 6 (Figure 5).

4.2.   Inclusion of spatial interaction (spatial explicit model)

Besides landuse option and annual precipitation, lateral exchange of surface water exhibits strong influence on phytomass production, vegetation and state composition.

Annual total phytomass - Annual total phytomass of all simulations ranged from 112 t per ha at high grazing intensity in 1992 to 983 t per ha at low grazing intensity in 2000 (Figure 3). Averaged

Figure 4: Time series of annual productivity for the simulated vegetation types. Medians of 500 simulation replicates are shown. Columns refer to different management scenarios (left: Gellap; right: Nabaos). Top row displays results for simulation moddels without spatial interaction and bottom row refers to simulation models including spatial interaction. Black circles refer to perennial grass, white circles to annual forbs, black triangles to dwarf shrubs and white triangles to shrubs.

over the timespan of 15 years total phytomass production at the scenario with low grazing intensity exceeds total phytomass production at the scenario high grazing intensity 2.24-fold. Linear regression analysis indicated that total phytomass at the scenario with low grazing intensity ($R^2 = 0.98$, p < 0.001) increased with annual precipitation. The same tendency is valid at the scenario with high grazing intensity ($R^2 = 0.98$, p < 0.001). Compared to the non-spatial model, total phytomass production simulated with the spatially explicit model is 2.61-fold higher at the scenario with low grazing intensity and 1.54-fold higher at the scenario with high grazing intensity.

Productivity of vegetation types – Not only total annual phytomass production is affected by spatial interaction, precipitation and landuse, but also productivity of the four most abundant vegetation types (perennial grass, annuals, dwarf shrubs and shrubs) (Figure 4). Including spatial interaction in simulating dynamics and productivity of these vegetation types has strongest impact at the scenario with low grazing intensity: perennial grass receives largest share in mean total productivity (47 %), followed by annuals (28 %), shrubs (19 %) and dwarf shrubs (6 %).

60
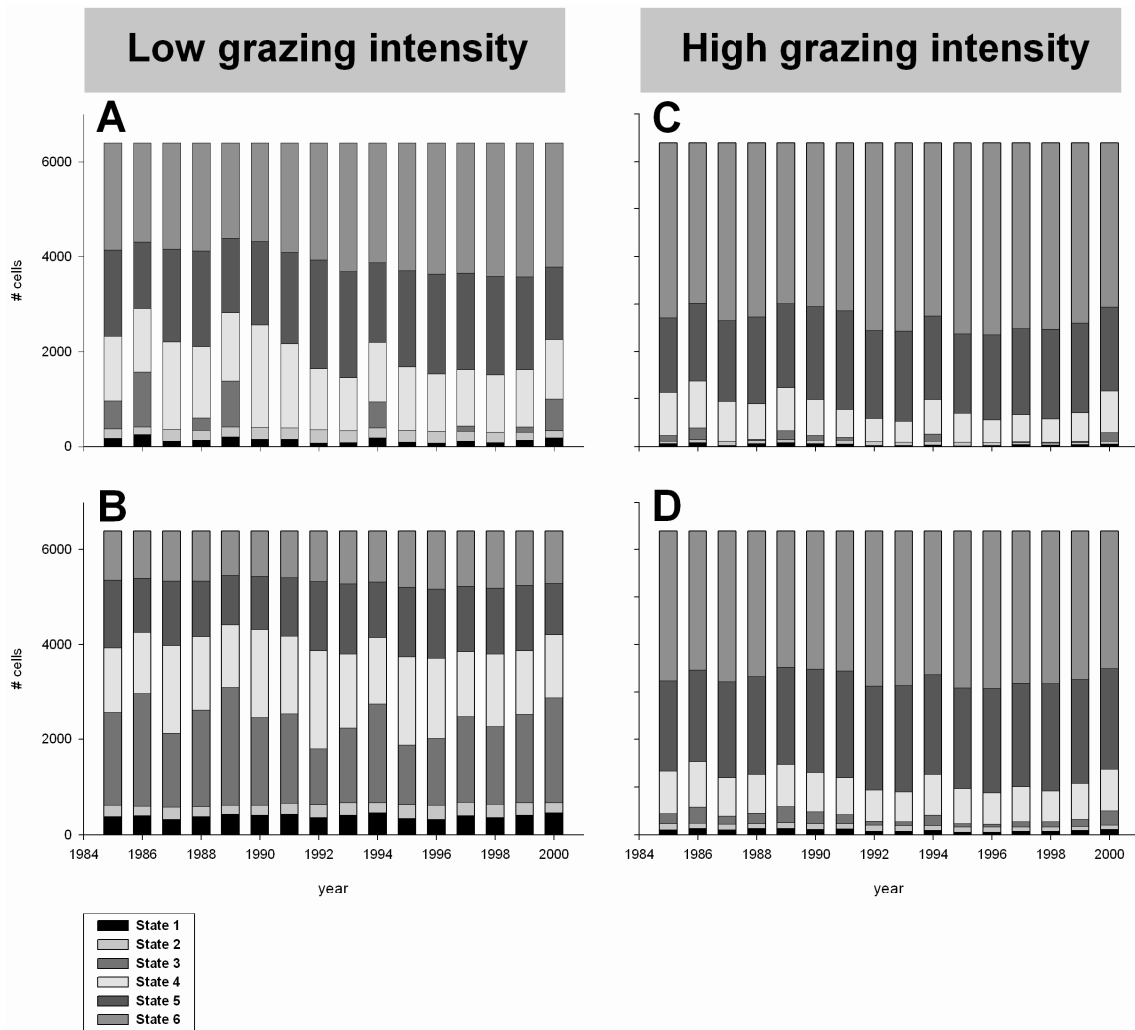
Figure 5: Time series of vegetation state composition. Vegetation state composition (left axis) is affected by spatial interaction, grazing as well as precipitation. Columns refer to different management scenarios (left: Gellap; right: Nabaos). Top row displays results for simulation moddels without spatial interaction and bottom row refers to simulation models including spatial interaction.

At the scenario with high grazing intensity, no effect of spatial interactions on the proportion of vegetation types in mean total productivity could be identified. Comparable to the non-spatial model version the proportion in mean annual total productivity was clearly decreased for perennial grasses (19 %) as well as dwarf shrubs (3 %) and dominance was shifted towards annuals (60 %) and shrubs (18 %).

Vegetation state composition - Figure 5 shows that spatial interaction at the scenario with low (L) as well as the scenario with high grazing intensity (H) heightens the number of cells (NC) in state 1 (L: 2.7-fold; H: 3.3-fold), 2 (L: 1.1-fold; H: 2.6-fold), and 3 (L: 4.7-fold; H: 1.7-fold) and leads to lower NC in state 4 (L: 0.8-fold; H: 0.8-fold) and 6 (L: 0.5-fold; H: 0.8-fold). In contrast to the

scenario with low grazing intensity (0.8-fold), NC in state 5 decreases at the scenario with high grazing intensity (1.8-fold).
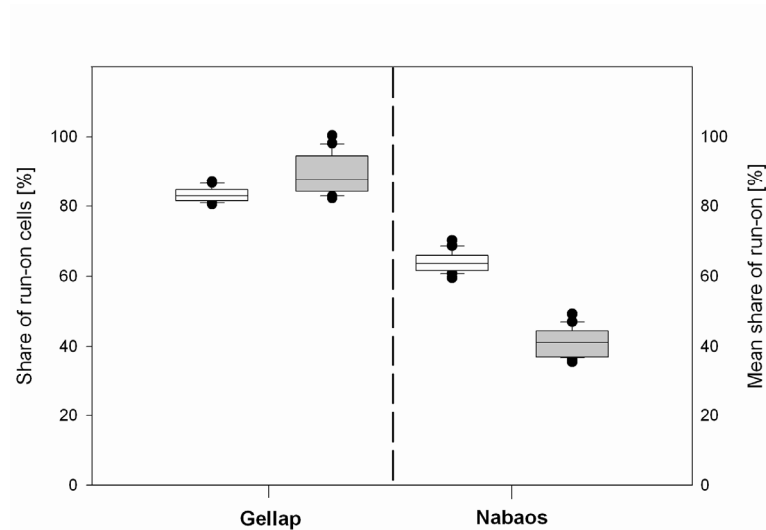
Figure 6: Effects of landuse on spatial interaction. At the scenario with low grazing intensity spatial interactions lead to high share of run-on cells (left axis, white boxplots) and high values of mean run-on (left axis, white boxplots). Mean run-on is given as % in total annual rain. In contrast, share of run-on cells as well as mean share of run-on at the scenario with high grazing intensity display low values.

Disturbance and spatial interactions – Disturbance in the form of overgrazing can have strong impact on lateral exchange of surface water (Figure 6). Light grazing intensities lead to 83 % of run-on cells in the total number of cells as well as high mean run-on in of these cells (85 %) for the years 1985 to 2000. In contrast, pr at the scenario with high grazing intensity decreases to 63 % with low mean run-on of 40 %.

4.3. Validation of simulated phytomass production

Measured I-NDVI - Vegetation at the communal rangelands (Nabaos) had lower I-NDVI than vegetation at the research farm (Gellap) across all growth seasons (Figure 7). The lowest value of 0.5 at the communal rangelands in 1987 contrasts with the highest value of 1.6 at the research farm in 2000. Averaged over the timespan of 15 years I-NDVI measured at the research farm exceeds I-NDVI measured at the communal rangelands 1.27-fold. Linear regression analysis indicated that I-NDVI is correlated with annual precipitation at the research farm ($R^2 = 0.81$, $p < 0.001$) and the communal rangelands ($R^2 = 0.91$, $p < 0.001$).

Comparison of simulated phytomass and measured I-NDVI – We compared simulated total annual phytomass with remotely sensed estimates of annual phytomass production (I-NDVI) to test if the landscape model displays vegetation dynamics in a simplified but realistic way. The linear

regression relationship between simulated total phytomass and I-NDVI (Figure 8) accounted for more variance at the spatial model ($R^2 = 0.79$, $p < 0.001$) than for the non-spatial model version ($R^2 = 0.69$, $p < 0.001$).
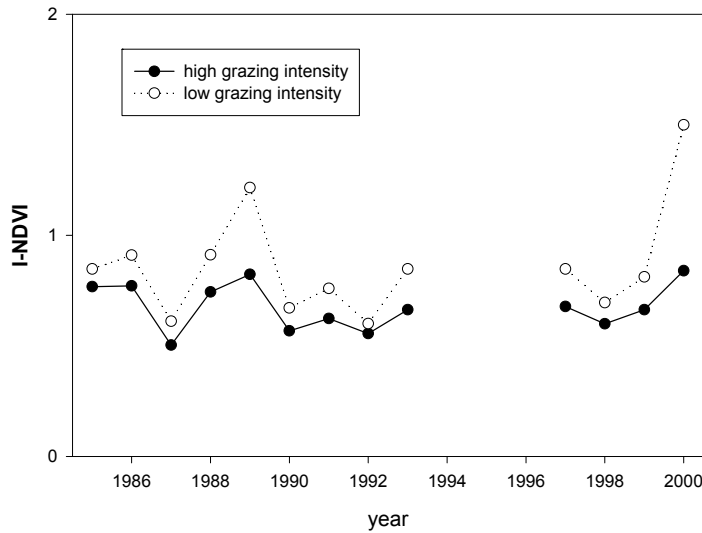
Figure 7: Time – Series of I-NDVI. I-NDVI (integrated normalized differential vegetation index) was calculated for each sampling-domain from seasonal summations (October to Septemper) of differences between NDVI and minimum NDVI from the seasons 1985/86 to 2000/01. Black circles represent the scenario with low grazing intensity (Gellap) and white circles represent the scenario with high grazing intensity (Nabaos).
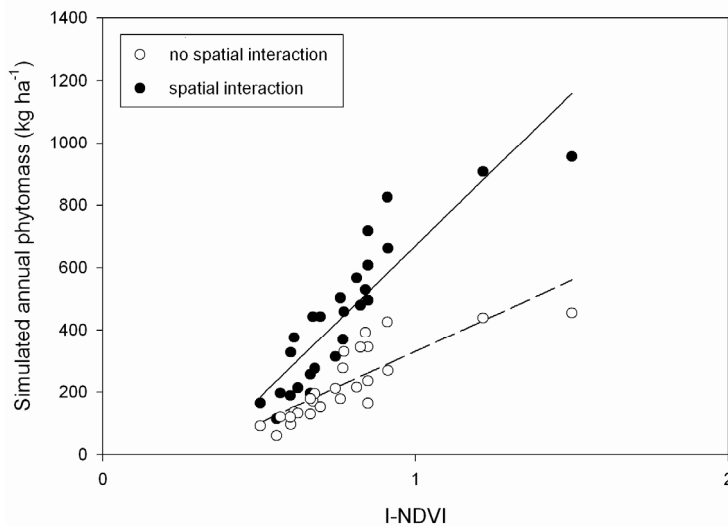
Figure 8: Comparison of simulated phytomass and measured I-NDVI. For both simulation methods and both management methods modelled total phytomass in each year from 1985 to 2000 were compared with remotely sensed indices of phytomass (I-NDVI). I-NDVI images cover 8km^2 of both, the research farm with low grazing intensity (Gellap) and communal rangeland with high grazing intensity (Nabaos).

5. Discussion

The aim of our study was to present a method which has the power to transfer and integrate existing information on vegetation dynamics and hydrological processes between spatial scales. Combining technologies of remote sensing and stochastic modelling, we successfully reproduced vegetation dynamics, composition and productivity that were 100 orders of magnitude larger. Using a small scaled simulation model the influence of exogeneous and endogeneous variables (vegetation state, precipitation, management and topography) on transition probabilities and phytomass production were estimated.

Until now, there are several limitations in the use of land use and landcover change applications. Transition probabilities of previous stochastic landscape models were estimated by using data observed and measured from empiric studies, air photography and remotely sensed images (e.g. Muller and Middleton 1994, Brown et al. 2000, Jenerette 2001, Weng 2002). Uncertainty in these studies remained relatively high because data was limited, i.e. transition probabilities were derived from short-term data (Baker 1989), microscale processes like ecohydrological feedback mechanisms and spatial interactions like surface water flow were not included.

The simulation results of our landscape model show that the explicit consideration of surface water flow can have strong impact on vegetation dynamics, composition and productivity at landscape scale. At low grazing intensity, a high number of run-on cells with high infiltration capacities serve as sinks for input by surface water flow. Spatial exchange of surface water among vegetation patches increases biomass production in comparision to simulations where spatial interactions were not considered. In contrast, disturbance in the form of overgrazing destabilizes positive feedbacks through vegetation and hydrology and therfore, decreases inflitration capacity of potential run-on cells. The buffer capacity of these hydrological sinks is reduced, run-off increases and biomass production remains low. The consideration of spatial interaction causes water downstream out of the simulated system and artificial droughts occur even in years with good precipitation.

This general process has been observed in other semi-arid and arid areas where the spatial exchange between patches of vegetation affects the resilience of ecosystems (van Koppel and Rietkerk 2004, Ludwig 2005). Ecosystems heterogeneous in space and linked by spatial interaction provide potential for buffering positive feedback. Coarse-scale catastrophic shifts are more likely in systems that have little spatial heterogeneity or no spatial feedback mechanisms to compensate for positive feedback. Taking these conclusions into account, our model results provide additional insights into the impact of spatial exchange of water on ecosystem service and functioning of arid rangelands. Spatial interaction does not only decrease total annual productivity but also affect vegetation composition. At low grazing intensities, the explicit consideration of spatial interaction favours high abundance of vegetation states with high cover of perennial grasses whereas vegetation

states with annual vegetation were frequent where spatial interaction of surface water flow was excluded. In contrast, only low effects of spatial exchange on vegetation composition could be observed at high grazing intensities (Nabaos). Here, vegetation states consist mainly of bare ground, shrubs and, in years of high precipitation, annuals dominate the simulated landscape at both model versions. Although our results demonstrate the high relevance of the explicit inclusion of spatial interactions at landscape scale for vegetation dynamics, until now they have seldom been recognised, quantified and incorporated into management decisions (Rastetter et al. 2003, van Koppel and Rietkerk 2004).

Here, we showed that an understanding of these interactions spatial exchange of surface water has important implications for improving the management of semi-arid and arid rangelands with distinct topgraphy. Generally, rotational grazing strategies have been proposed to increase stocking capacity, improve animal gains, and improve forage production and range condition (e.g. Fynn and O'Connor 2000). In semi-arid and arid rangelands with distinct topgraphy the rotation of livestock between different paddocks combined with moderate stocking rates becomes even more important as non-degraded paddocks serve as hydrological sinks which catch and conserve surface run-off from degraded paddocks with low vegetation cover. Therefore, downstream out of the simulated system and 'artificial droughts' are prevented, the system keeps its buffer capacity and efficient use of water resources is guaranted at all times.

6. References

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7. Link to the proceeding chapter

In the previous two chapters, I analyzed the impact of disturbance by grazing on vegetation dynamics and coupled hydrological processes at muliple spatial scales. I showed that an omission of eco-hydrological processes may directly affect the accuracy of predictions.

However, the development of sustainable grazing strategies for semi-arid and arid rangelands does not only require a comprehensive understanding of the interplay between ecological and hydrological processes on different scales but also an inclusion of the complex interactions between land use and vegetation dynamics.

In the last chapter I will present an integrated ecological-economic approach that consists of an ecological and an economic module and combines relevant processes on either level. Vegetation dynamics and forage productivity for both modules is derived by the small-scaled vegetation model. Based on this I will investigate the importance of farmers' knowledge on how the ecosystem works in times of climate change.

5 Landuse experience does not qualify for adaptation to climate change [1]

1. Abstract

The need to implement sustainable resource management regimes for semi-arid and arid rangelands is acute as non-adapted grazing strategies lead to irreversible environmental problems such as desertification and associated loss of economic support to society. In these sensitive ecosystems, traditional sectoral, disciplinary approaches will not work to attain sustainability: achieving a collective vision of how to attain sustainability requires interactive efforts among disciplines in a more integrated approach.

Therefore, we developed an integrated ecological-economic approach that consists of an ecological and an economic module and combines relevant processes on either level. Parameters for both modules are adjusted for an arid dwarf shrub savannah in souththern Namibia. The economic module is used to analyze decisions of different virtual farmer types on annual stocking rates depending on their knowledge how the ecosystem works and climatic conditions. We used a dynamic linear optimization model to simulate farm economics and livestock dynamics. The ecological module is used to simulate the impact of the farmers' land-use decision, derived by the economic module, on ecosystem dynamics and resulting carrying capacity of the system for livestock. Vegetation dynamics, based on the concept of State-and-transition models, and forage productivity for both modules is derived by a small-scale and spatially explicit vegetation model. This mechanistic approach guarantees that data collected and processes estimated at smaller scales are included in our application. Simulation results of the ecological module were successfully compared to simulation results of the optimization model for a time series of thirty years. We revealed that sustainable management of semi-arid and arid rangelands relies strongly on rangeland managers' understanding of ecological processes. Furthermore, our simulation results demonstrate that the projected lower annual rainfall due to climate change adds an additional layer of risk to these ecosystems that are already prone to land degradation.

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[1] A version of this chapter has been submitted to *Agriculture, Ecosystems & Environment* as: A. Popp, S. Domptail, N. Blaum, F. Jeltsch: Landuse experience does not qualify for adaptation to climate change

2. Introduction

Semi-arid and arid ecosystems cover about 30% of the world's land surface, occur in all continents and are inhabited by 1.10 billion people which is approximately 20% of the global population (Stafford Smith 1996, Sivakumar et al. 2005). Livestock production is the most important type of land use. As the productivity of dryland vegetation is primarily determined by low annual rainfall, the amount of rainfall strongly influences carrying capacity of livestock (Noy-Meir 1973, Schlesinger et al. 1990, Chesson et al. 2004).

Ecosystem management is a systems approach to the management of natural resources (Dale et al. 2000). It is a process of land-use decision making that takes into account the full suite of organisms and processes that characterize and comprise the ecosystem and is based on the best understanding currently available how the ecosystem works (Dale et al. 2000, Olsson and Folke 2001, Gunderson and Holling 2002, Olsson et al. 2004). Particularly, in sensitive ecosystems such as semi-arid and arid rangelands, sustainable management of resources and high economic returns are achieved by perfect farmers' ecological knowledge and foresight of the environment. However, there is a great mismatch between the kinds of ecosystems that farmers want and the kinds of ecosystems that are attainable (Carpenter and Gunderson 2001): Farmers tend to overestimate the amount of annual rainfall as they ignore ecological expertise to serve narrow interest like short-term income. Resulting non-adapted grazing strategies may lead to irreversible environmental problems like desertification and associated loss of economic support to society (UNEP 1995).

Observed and predicted future climatic changes significantly affect natural and managed ecosystems (Adams et al. 1989, Hughes et al. 2003, Root et al. 2003, Parmesan and Yohe 2003, Weltzin et al. 2003): A reduction in mean annual rainfall as predicted by climate models for the subtropical latitudes (Karl et al., 1995, Easterling et al. 2000, IPCC 2001, IPCC 2007) will likely lead to a general decrease in the grass resource and increased dryland vulnerability to degradation. Therefore, sustainable management strategies must continually be updated and adjusted (Salinger et al. 2005, Sivakumar et al. 2005). Failure to account for human adaptations will overestimate the potential damage from climate change and underestimate its potential benefits.

We have developed and used a bio-economic simulation method to evaluate the effects of farmer's ecological knowledge on ecosystem dynamics and linked human actions in a grazing system in arid southern Namibia. We first analyzed the impact of the virtual farmer's strategy choice under current climatic conditions and secondly investigated the importance of adapting current grazing strategies to climate change to maintain the rangeland system as an income base.

Our integrated bio-economic approach consists of an ecological and an economic module which are equally strong and detailed. Vegetation dynamics, based on the concept of State-and-transition

models, and forage productivity for both modules is derived by a small-scale and spatially explicit vegetation model (*TOPMAN*). This mechanistic approach guarantees that data collected and processes estimated at smaller scales are included in our application. The economic module is used to analyze decisions of different virtual farmer types on annual stocking rates depending on their knowledge how the ecosystem works and climatic conditions. We used a dynamic linear optimization model to simulate farm economics and livestock dynamics. All parameters determining herd dynamics, variable and fixed costs and product prices are the mean for the farmers of the study area.

The ecological module is supplied with the management behaviour of the different farmer types, estimated by the economic module. By the help of the ecological module we simulate vegetation dynamics, annual productivity of herbaceous and woody vegetation and resulting numbers of livestock under current and future climatic conditions.

Aim of our study is (i) to evaluate how farmers' landuse experience and ecological knowledge affects tightly coupled ecological and economic systems of arid grazing systems and (ii) to investigate the importance of adapting rangeland mangement to climate change. To verify that our combined bio-economic modelling approach is generally able to display optimal decision making over time we compared simulation results of the ecological module for vegetation composition, productivity and stocking rates with simulation results of the economic module for a time series of thirty years (1973 – 2003).

3. Methods

3.1. Study area

The study region is located in the Nama-Karoo in southern Namibia. Rainfall throughout the entire region is erratic and highly variable with a mean of 150 mm. Rainfall events often occur as isolated thunderstorms (Heyns et al 1998). High evaporation rates are measured due to high daytime temperatures up to 37° C (Namibian Meterological Service 2000). The Nama-Karoo vegetation is greatly restricted by water availability. Vegetation cover is low and when heavily grazed, perennial grasses (e.g. *Stipagrostis spp.)* greatly valued as forage are replaced by annual grasses (e.g. *Schmidtia kalahariensis*) and unpalatable shrubs (e.g. *Rhigozum trichtomotum*) (Kuiper and Meadows 2002). About 80% of the research area is privately and commercially farmed by small livestock (mainly sheep and goats).

3.2. Bio-economic model

The bio-economic approach consists of an ecological and an economic module. It describes the evolution of a typical farm for the study area with the size of 10.000 hectares. Each hectare is specified by its vegetation state (Table 1).

Table 1: Definition of vegetation states for the research area. Panels in the column headers refer to cover (%) of the respective vegetation type (PG = perennial grass; W = woody vegetation). Pannels in the row headers refer Vegetation State, enumerated by one to six.

|	$Cover_{PG}$ (%)	$Cover_W$ (%)
State 1	30 – 100	40 – 100
State 2	0 – 29	40 – 100
State 3	50 – 100	0 – 40
State 4	10 – 49	0 – 40
State 5	0 – 9	10 – 40
State 6	0 – 9	0 – 9

Both modules proceed in annual time steps over a time horizon of thirty years. Vegetation dynamics, based on the concept of State-and-transition models (Westoby et al. 1989), and forage productivity for both modules is derived by a small-scale and spatially explicit vegetation model (*TOP-MAN*, for more details see chapter 1).

The economic module is based on a linear optimization model that simulates farm economics and livestock dynamics (Domptail et al. submitted). All parameters determining herd dynamic, variable and fixed costs and product prices are the mean for the farmers of the study area. The basic concept of such mathematical programming is to maximise profit by determining optimal decision making over time (e.g. Batabyal 1999, van Wenum et al 2004, Okumu and al 2004). We used the economic module to supply decisions of the virtual farmer on annual stocking rates depending on its knowledge how the ecosystem works. Therefore, we analysed 600 simulation years to estimate farmers' land-use decision making, i.e. vegetation state-specific stocking rates, in relation to annual water availability and vegetation state composition within the farm (see below for detailled description). Vegetation state composition is classified by the sum of hectares in each vegetation state. Here, we

simply distinguish between vegetation states occupying more than 5000 ha and vegetation states occupying less than 5000 ha.

The ecological module is used to simulate the impact of the farmers' land-use decision, derived by the economic module, on ecosystem dynamics and resulting carrying capacity of the system for livestock under current and future climatic conditions.

Figure 1 gives an overview of our ecological-economic modelling approach
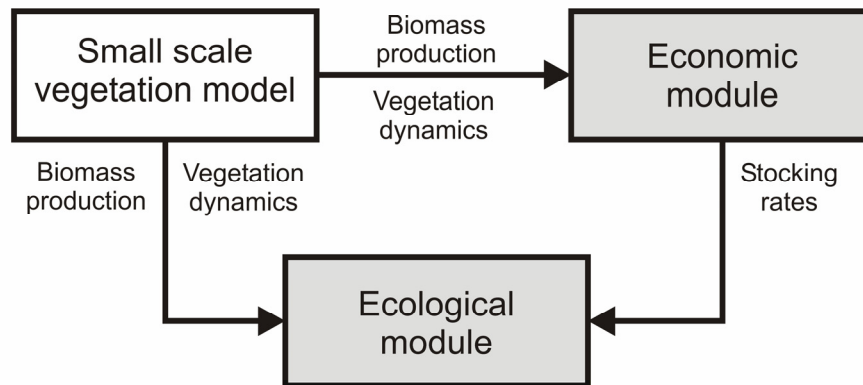
Figure 1: Visualisation of the bio-economic modelling approach. We used a small-scale and spatially explicit vegetation model to derive data for vegetation dynamics and forage productivity for the economic optimization module and the ecological module. The economic module is used to analyze decisions of different virtual farmer types on annual stocking rates depending on their knowledge how the ecosystem works and climatic conditions. The ecological module is used to simulate the impact of the farmers land-use decision, derived by the economic module, on ecosystem dynamics and resulting carrying capacity of the system for livestock.

3.2.1. Vegetation dynamics

We used a state and transition approach to simulate vegetation dynamics (Westoby et al. 1989). State and transition models provide a relatively simple, management-oriented way to classify land condition (state) and to analyse the impact of factors that might cause a shift to another state (transition). Together with Namibian rangeland experts (farmers and extension officers), we first identified six vegetation states where each state is related to the percent cover of shrubs and perennial grass (Table 1). Afterwards, we used the small scale model TOPMAN to calculate annual transition probabilities between each state for different classes of rainfall and stocking rate. Water availability was classified in four categories of annual rainfall: 1=poor (<100 mm), 2=moderate (100-139 mm), 3=good (140–179 mm) and 4=very good (>180 mm).

Transition probabilities were calculated as Markovian stochastic processes (Markov 1907): a state at time t depends on the state at time t-1 and the impact of exogenous factors water availability, slope and present landuse. A m x m transition matrix (P) contains the conditional probabilities p_{ij} that a cell in State i at time t will transition to state j at time $t+1$. For m states P has the form:

$$
P = \begin{bmatrix} p_{11} & p_{12} & \cdots & p_{1m} \\ p_{21} & p_{22} & \cdots & p_{2m} \\ \cdots & \cdots & \cdots & \cdots \\ p_{m1} & p_{m2} & \cdots & p_{mm} \end{bmatrix}
\tag{1}
$$

P is row-standardized, such that the sum of transition probabilities from a given state is always equal to one:

$$
\sum_{j=1}^{m} p_{ij} = 1 \quad i = 1, 2, \ldots, m
\tag{2}
$$

The states $p(t)$ at time t can be calculated by:

$$
p(t) = p(t-1) \cdot P
\tag{3}
$$

We derived transition probabilities by calculating transition probabilities of the process based small-scale simulation model. Maximum likelihood estimates of the transition probabilities (Anderson and Goodman 1957) are then:

$$
p_{ij} = \frac{n_{ij}}{\sum_{j=1}^{n} n_{ij}}
\tag{4}
$$

Where n_{ij} is the simulated number of transitions from State i to State j. To gain these values we run the small-scale model for 100 years with 500 repetitions.

Generally, we assume that (i) transition probabilities are constant over time and (ii) transitions are spatially independent. An approach to model nonstationarity is to switch between different stationary matrices (Rejmanek et al. 1987). Thus, to consider variability in space and time of transition probabilities related to water availability, slope and land use option we generated transition matrices for all combinations of these exogenous factors.

3.2.2.   Productivity

Annual phytomass production of the four vegetation types depends on the cells slope, present vegetation state and water availability. For each vegetation type we calculated productivity coefficients from multiple linear regressions of biomass on slope, vegetation state and water availability derived from the small scale model.

3.2.3.   Small-scale simulation model

Transition probabilities and phytomass production are derived from a small scale simulation model. In the following we give an overview of the parameters and processes included. A detailed model description has been presented in chapter 1.

The spatially-explicit and individual based model simulates the vegetation dynamics of an 1 ha area (100 x 100 m^2, 33 x 33 cells). Cell size is 3 m x 3 m, that corresponds to the maximum observed diameter of a shrub. Woody plants are simulated individually and each cell contains a list of plant individuals. Herbaceous vegetation (perennial grass and annuals) are treated as matrix plants, and a cell is either occupied or not. Slope angle is included by decreasing elevation values of the cells towards one side of the landscape. For each cell, water availability, establishment, phytomass production, grazing and mortality are simulated in annual time steps

Water availability - Cell-specific water availability of the different vegetation types is influenced by rain, evaporation and competition. Soil texture and vegetation cover have an impact on evaporation reducing soil water content in the upper soil layer. Competitive effects of vegetation reduce the water availability for establishment and, in cells with overlapping root systems, vegetation has a competitive effect on the neighbouring vegetation types.

Establishment - The cells' probability of successful establishment for the vegetation is determined by site-specific probabilities of seed and water availability as well as the probability to survive grazing.

Growth - Biomass production of the herbaceous vegetation is related to a rainfall-grass production relationship of diverse southern African savanna regions (e.g. Higgins, 2000). In contrast, annual biomass production of woody plant individuals depends on water availability and current height performance.

Grazing - The small scale model simulates grazing and browsing on herbaceous and woody vegetation. Vegetation types differ in their palatability for grazers and browsers. What and to which amount a plants biomass will be consumed depends on the relation of available and needed forage as well as its specific palatability.

Mortality - Survival of perennial plants is determined by water availability and livestock grazing (O'Connor, 1994; Milton and Dean, 2000). Here, the probability to survive is related to the plants performance, since disturbances as drought or overgrazing have strong influence on productivity. Within the group of perennial plants differences among species in disturbance tolerance results in better physiological adaptations to disturbance.

3.2.4.   Livestock dynamics

The major management task for a farmer in our research area is to adjust livestock density in order to maximize net benefits from meat and wool production.

For the dynamics of livestock, the herd size (L_t) on the farm at time t, is limited by total available forage. The farmer can buy (b_t) or sell (s_t) livestock. Furthermore, S_t can grow due to its own density dependent growth process:

$$L_{t+1} = L_t + g_S * L_t \left(1 - \frac{L_t}{C_t}\right) - s_t + b_t \tag{5}$$

Here g_s is the biological growth rate of the livestock population and C_t is the farm's carrying capacity at time t. C_t is in turn defined by the consumption rate of livestock (c), and the available annual forage (F_t).

$$C_t = \frac{F_t}{c} \tag{6}$$

3.2.5.   Optimisation

A farmer will choose the grazing management strategy which maximises his utility function. We assume that the farmer's utility depends on economic values, i.e. its income.

Economic utility (e) is determined by income and costs, which is a function of the number of animals bought and sold, and the costs of labour. The income derived is determined by p, the price of the livestock product, and s_t, the number of livestock sold at time t. Costs are incurred by the number of livestock purchased at time t (b_t).

Furthermore, farmers have access to financial markets and use credit possibilities. Interest profit (I_P) and loss of interest (I_L) are derived by the interest rate r_i of 4 %, the discount rate r_d of 14 % and e_{t-1}, the balance of the former year. I_P ($I_P = r_i * e_{t-1}$) occurs if e_{t-1} exceeds 0, whereas I_L ($I_L = r_d * e_{t-1}$) is considered if falls below 0. The income and cost parameters together define e, the economic index at time t as,

$$e_t = p(b_t - s_t) + I_P - I_L \tag{7}$$

The economic utility over a planning horizon T, U_{econ} is,

$$U_{econ} = \sum_{t=1}^{T} e_t \tag{8}$$

3.3. Simulation analysis

Annual rainfall is the most important variable in the considered agro-ecological system because it affects vegetation dynamics, the effects of stocking rate on rangeland condition and determines the yearly available biomass.

We used the bio-economic model to test the impact of farmer's knowledge on how annual rainfall affects the tightly coupled ecological and economic systems of an arid dwarf shrub savannah in southern Namibia. Therefore, we compare optimal solutions for farmers with perfect knowledge how the ecosystem works (F_{PK}) and optimistic farmers which overestimate (F_O) the positive effects of annual rainfall on ecological processes by assessing the actual rainfall class one category higher.

In doing so, we first used a time series of rainfall data for the years 1973 to 2003 (Namibian Metereological service unpubl. data) to simulate vegetation dynamics, biomass production for herbaceous and woody vegetation and stocking rates for each type of farmer.

Then, we will summarize the impact of farmers' knowledge for present and future climatic conditions on the agro-ecological system. Under scenarios of intermediate global warming, most climate models predict significant decreases in mean annual rainfall in southern Africa by 5 to 15% (IPCC 2001). Accordingly, we reduce each value of annual rainfall by 10% for the climate change scenario. We present mean productivity, mean stocking rate of the last and the future 30 years and final condition of the rangeland.

3.4. Validation

The economic module, based on linear optimization, reveals optimal management decisions (see above for detailed description). The ecological module in turn is used to simulate the impact of these land-use decision on ecosystem dynamics and resulting carrying capacity of the system for livestock under given side-conditions.

To verify that our combined bio-economic modelling approach is generally able to display optimal decision making over time we compared simulation results of the ecological module for vegetation composition, productivity and stocking rates with simulation results of the economic module for a time series of thirty years (1973 – 2003). Land use decisions and vegetation dynamics for both models are based on rainfall data from the Keetmanshoop weather station (source: unpublished data from the Weather Bureau Windhoek, Namibia).

4. Results

4.1. Ecological kowledge

In general, farmers' decisions on state specific stocking rates are closely connected to its rainfall perception and vegetation composition (Figure 2).
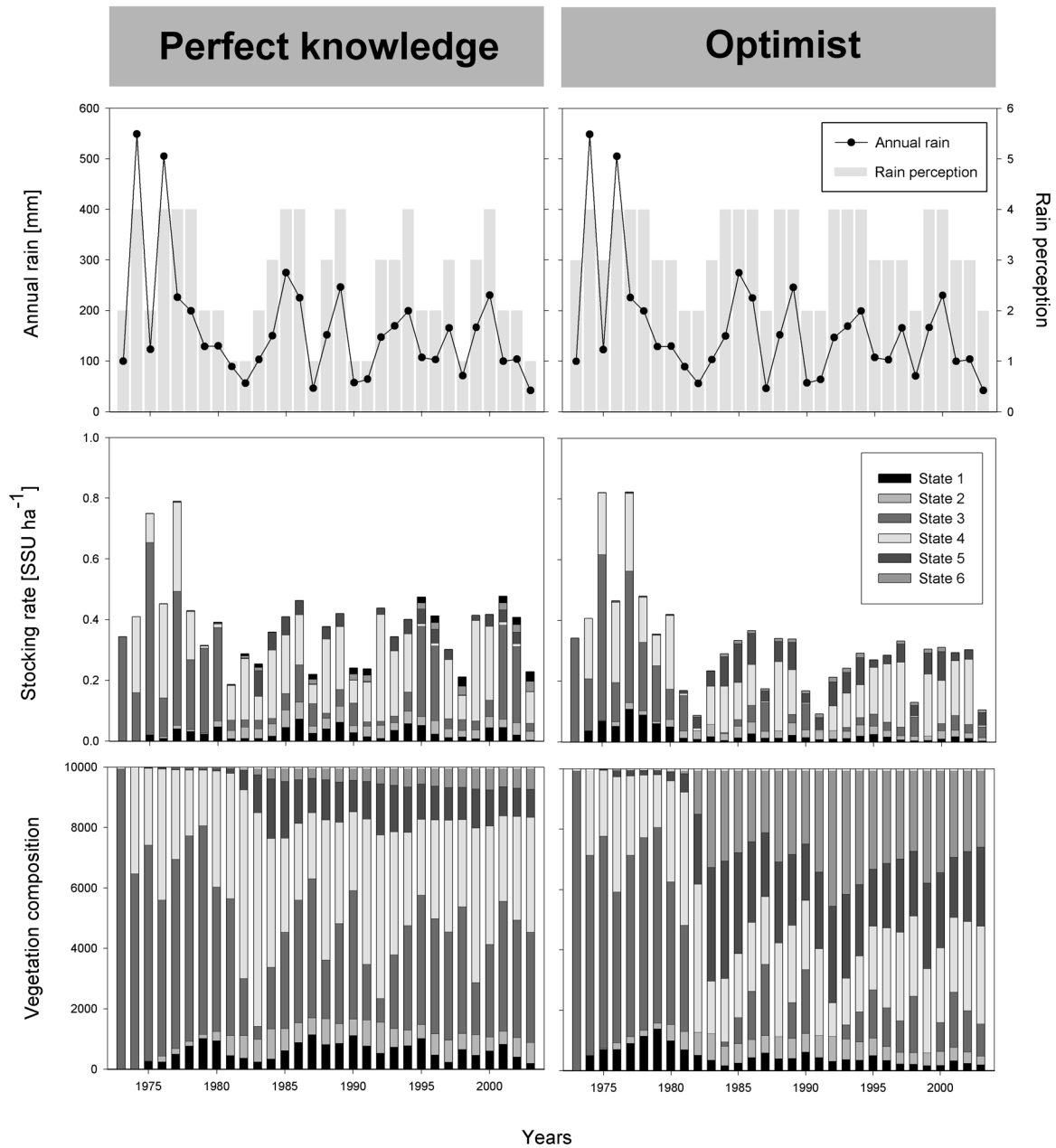

Figure. 2: Time series of annual precipitation, farmers' rain perception, stocking rate and vegetation state composition. Upper row shows annual precipitation (left axis) and its subdivision into farmers' rain percep-tion (right axis) (left: farmer with perfect knowledge; right: optimistic farmer). Rainfall of a given year was categorized as poor (1), moderate (2), good (3) and very good (4). Row in the middle shows vegetation state specific stocking rate and bottom row shows vegetation state composition.

In the beginning (years 1973 – 1982), the virtual farmer with perfect knowledge (F_{PK}) mainly stocks livestock on State 3 and State 4, reflecting the dominance of these vegetation states. In a drought period (years 1982 and 1983) livestock numbers are generally decreased and stocking on State 3 is avoided. Nevertheless, State 5 and 6 gain prominence and in the following years dominance is shifted between State 3 and 4 in subject to annual rainfall. Generally, high stocking on State 3 only occurs if high abundance of State 3 (> 5000 ha) coincides with medium rain perception (years 1995, 1996, 2001 and 2002). Elsewise, F_{PK} primarily stocks on State 4.

Stocking decisions of the optimistic virtual farmer (F_O) are different. He also decreases total livestock numbers in the first drought period (years 1982 and 1983), but in contrast to F_{PK} he mainly stocks on State 3. Hereafter, the amount of State 5 and State 6 increases in comparison to F_{PK} by 100 % and 462 % over the last 20 years. In comparison to F_{PK}, the amount of hectares in State 4 is decreased by 63 %

State 3 appears only in years with high annual rainfall (years 1984, 1985, 1989, 1994, and 2000), whereas application of high stocking rates on State 3 decreases the number of hectares in this state rapidly.

Based on the vast degradation of the rangeland, mean total stocking rate applied by F_O after the first drought period is decreased by 66 % in comparison to F_{PK}.
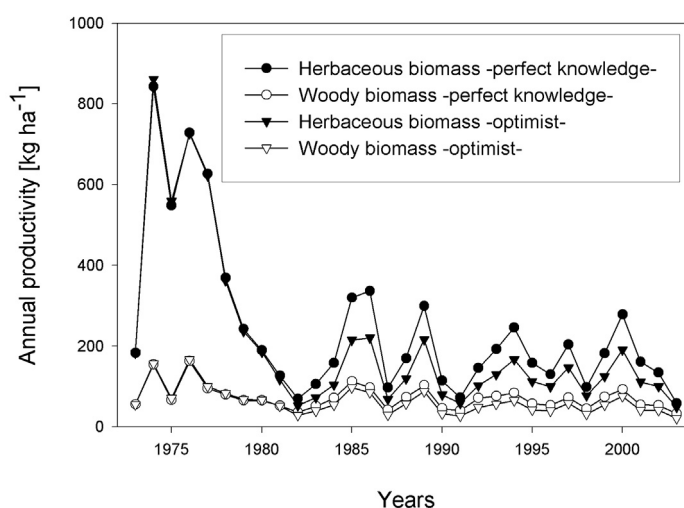

Figure 3: Time series of annual productivity. Black circles refer to herbaceous annual biomass production based on the management decisions of farmers with perfect knowledge, white circles to herbaceous annual biomass production based on the management decisions of optimistic farmers, black triangles to woody annual biomass production based on the management decisions of farmers with perfect knowledge and white triangles to woody annual biomass production based on the management decisions of optimistic farmers.

Land degradation is also reflected by annual productivity of herbaceous and woody vegetation (Figure 3). Annual productivity of herbaceous vegetation on the farm of F_O is decreased by 41 % in comparison to F_{PK} and annual productivity of woody vegetation by 33 % over the last 20 years.

4.2. Validation

Afterwards simulation results of the ecological model for vegetation composition, productivity of herbaceous and woody vegetation and annual total stocking rates are compared to simulation results of the economic module (Figure 4) for a time series of thirty years. The correlation coefficients between the two data series for vegetation composition ($R^2 = 0.97$), productivity of herbaceous ($R^2 = 0.98$) and woody vegetation ($R^2 = 0.92$) and annual total stocking rates ($R^2 = 0.67$) indicates that our integrated bio-economic modelling approach is generally able to display optimal decision making over time.
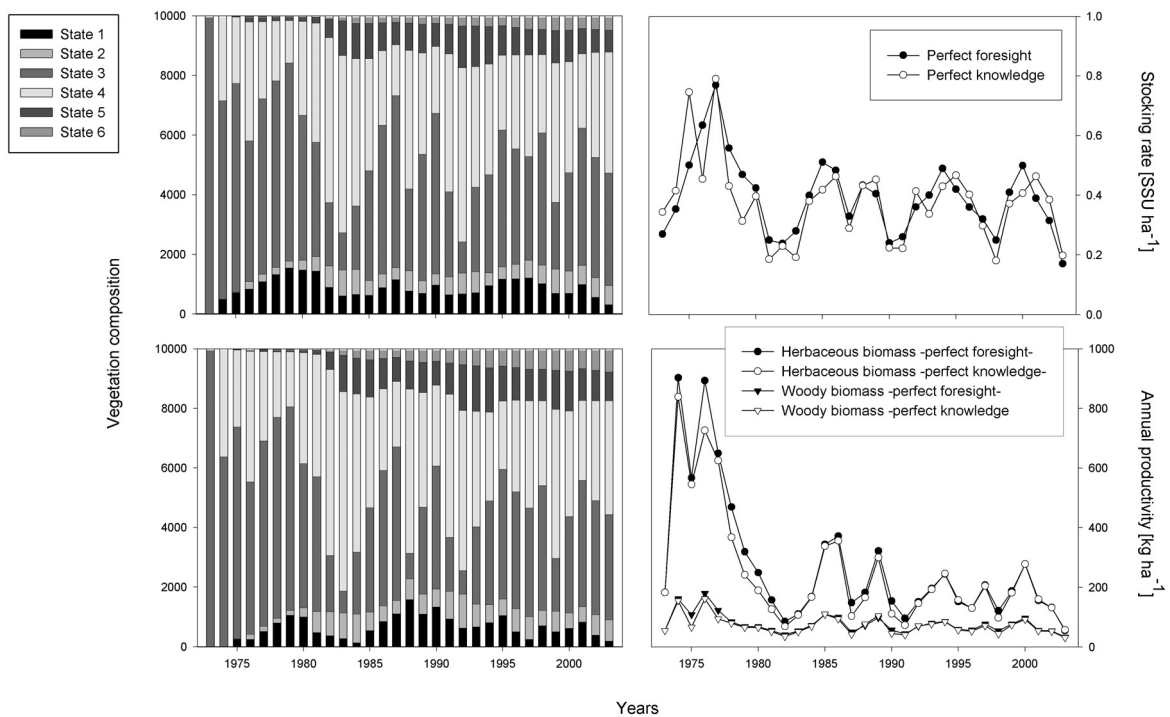
Figure 4: Validation of the bio-economic modelling approach. Vegetation state composition, productivity of herbaceous and woody vegetation and annual total stocking rates of the ecological module are compared with the simulation results of the optimization model (1973 – 2003). Rainfall data are used from the Keetmanshoop weather station (source: unpublished data from the Weather Bureau Windhoek, Namibia).

4.3. Adaptation to climate change

Decreasing annual precipitation due to climate change affects vegetation composition (Figure 5), productivity (Figure 6) and livestock numbers (Figure 5). A farm managed by a farmer with perfect knowledge (PK) based on ecosystem dynamics of the past (P) and related to rainfall of the past 30 years (F_{PK_PP}) leads to mean herbaceous biomass production of 246 kg ha^{-1} and mean woody biomass production of 72 kg ha^{-1}. Mean annual total stocking rate is 0.337 SSU ha^{-1} and vegetation composition in the final year is dominated by State 3 (3712 hectares) and State 4 (3622 hectares). In contrast, a farm managed by a farmer with perfect knowledge based on predicted future ecosystem dynamics (F) and related to predicted future rainfall (F_{PK_FF}) decreases mean herbaceous biomass production by 13 % and mean annual total stocking rate by 7 %. Woody biomass production is barely affected and vegetation composition in the final year is dominated by State 4 (5316 hectares).
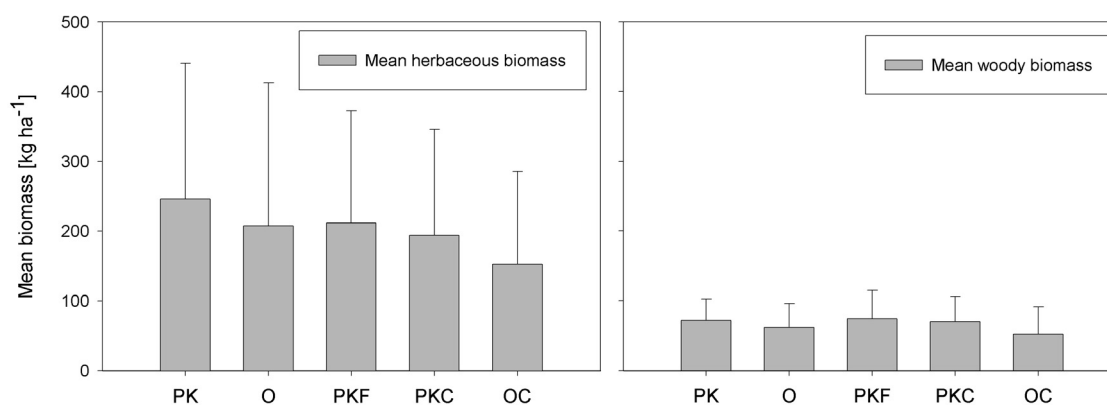
Figure 5: Impact of farmers' knowledge on mean annual productivity under past and predicted climatic conditions. Grey bars refer to mean biomass production of herbaceaous vegetation (left) and woody vegetation (right) within 30 years. F_{PK_PP} stands for a farmer with perfect knowledge based on past ecosystem dynamics and related to past rainfall, F_{O_PP} stands for an optimistic farmer with knowledge based on past ecosystem dynamics and related to past rainfall, F_{PK_FF} stands for a farmer with perfect knowledge based on future ecosystem dynamics and related to future rainfall, F_{PK_PF} stands for a farmer with perfect knowledge based on past ecosystem dynamics and related to future rainfall, FO_PF stands for an optimistic farmer with knowledge based on past ecosystem dynamics and related to future rainfall.

However, non-adapted grazing strategies like overestimation of annual precipitation can enhance the negative effects of climate change. Compared to F_{PK_FF} only minor shifts towards lower mean herbaceous biomass production (8 %), mean woody biomass production (6 %) and annual total stocking rate (6 %) did occur for the farmer with perfect knowledge based on ecosystem dynamics

of the past and related to predicted future rainfall (F_{PK_PF}). Composition of vegetation states is barely affected.
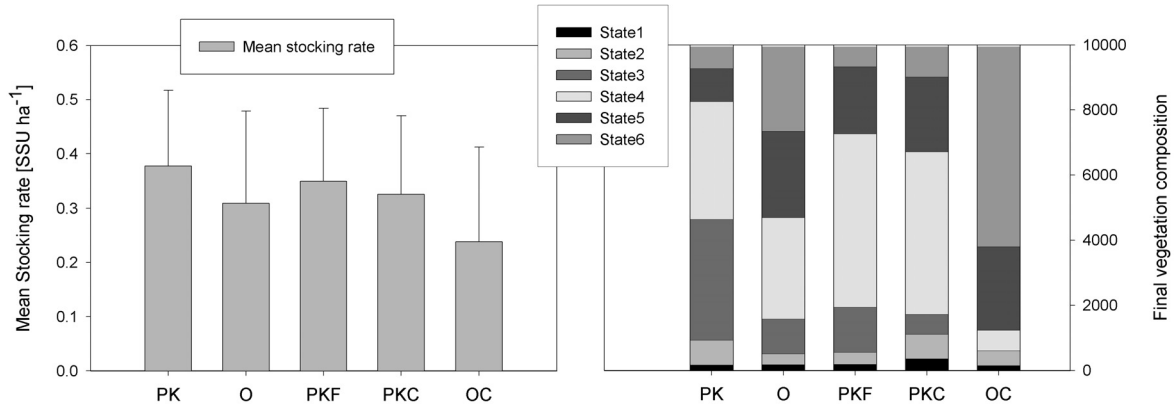
Figure 6: Impact of farmers' knowledge on mean stocking rate and final vegetation composition under past and predicted climatic conditions. Grey bars refer to mean biomass stocking rate (left) within 30 years and . F_{PK_PP} stands for a farmer with perfect knowledge based on past ecosystem dynamics and related to past rainfall, F_{O_PP} stands for an optimistic farmer with knowledge based on past ecosystem dynamics and related to past rainfall, F_{PK_FF} stands for a farmer with perfect knowledge based on future ecosystem dynamics and related to future rainfall, F_{PK_PF} stands for a farmer with perfect knowledge based on past ecosystem dynamics and related to future rainfall, $FO_{\_PF}$ stands for an optimistic farmer with knowledge based on past ecosystem dynamics and related to future rainfall.

A different picture shows for the farmer which overestimates the impact of annual rainfall on ecosystem processes (*O*) based on ecosystem dynamics of the past and related to predicted future rainfall ($FO_{\_PF}$). Here, compared to F_{PK_FF}, mean herbaceous biomass production is decreased by 72 %, mean woody biomass production by 70 % and mean annual total stocking rate by 68 %. No hectares in State 3 are existent in the final year and vegetation composition is dominated by State 6 (6198 hectares) and State 5 (2596 hectares).

5.   Discussion

The driving reason for our study was to get a better understanding of the complex interactions of socio-ecological systems as a basis for sustainable long-term management of arid rangelands.
The study of such human-environment interactions is necessarily interdisciplinary in character (Carpenter 2002, Benett et al. 2004). Both, ecologists and economists use simulation models, but mostly these models are disciplinary in nature and therefore exhibit clear limitations (Perrings 2002). To overcome these limitations, we developed an ecological and an economic simulation module and linked these two different traditions of modelling. This linkage allows a balanced modelling approach that combines relevant processes on either level. By the help of this linkage, we

have analyzed the relevance of the farmers' ecological knowledge for longterm functioning of a grazing system in southern Namibia under current and future climate conditions.

The simulation results of our integrated bio-economic approach show that sustainable management of semi-arid and arid rangelands relies on the farmers' perception on how the ecosystem works. A farmer with perfect knowledge uses stocking rates which guarantee long-term functioning of the tightly coupled socio-ecological system. Degradation i.e. shifts to vegetation states with low herbaceous cover as well as low productivity of herbaceous and woody vegetation is prevented. In contrast, an optimistic farmer overestimates the positive effects of annual rainfall on vegetation dynamics. Particularly in years with low annual rainfall, he applies stocking rates that lead to vast degradation. Dominance of vegetation states with low herbaceous and woody vegetation cover lead to much lower productivity and stocking rates even in years with high annual rainfall. In addition to low numbers of livestock, longterm income is reduced as mismanagement has severe impact on the sale value of the rangeland.

Our results are in line with the assumption that a lack of knowledge is generally an obstacle for effective implementation of sustainable rangeland management (Buxton and Stafford Smith 1996). Subsidiary, Janssen et al. (2004) reported that, in comparison to a rangeland manager with perfect knowledge, possible expected returns from grazing activity are reduced by one third for rangeland managers that ignore rainfall variability. But mismanagement is not only a lack of knowledge, to which the answer would be either more research or better transfer of knowledge to rangeland managers. In many cases rangeland managers are insufficiently engaged to adopt even if adequate knowledge does exist as they behave to maximise their short-term profit (Carpenter and Gunderson 2001). Here, my simulation model, which is clearly only a caricature of the real complex system, might nevertheless serve as a tool that enables to present the long-term consequences of different management decisions.

However, ecosystems and the services they provide are changing, often in ways farmers cannot anticipate. Therefore, sustainable management is not just a set of well-known and established practices, rather a process requiring skills of adaptability (Wall and Smit 2005). Such adaptation skills determine how vulnerable a specific system is to external or internal stresses, such as climate change (Carpenter et al. 2001, Füssel and Klein 2006). In general, our model shows that decreasing annual precipitation due to climate change affects vegetation composition, decreases herbacaeous and woody productivity and livestock numbers even for a farmer with perfect knowledge of future climate conditions. Mismanagement enhances these negative effects of climate change. Management that is based on perfect ecological knowledge of the past shows minor effects compared to management that is based on perfect ecological knowledge of future climate change. In contrast, management that is based on overestimating the effect of annual rainfall enhances degradation by shifting the dominance of vegetation states towards states with marginal herbaceous and woody cover and high proportions of bare ground.

Here, we showed that sustainable management of semi-arid and arid rangelands relies strongly on the farmers' knowledge on how the ecosystem works. Furthermore, our simulation results indicate that the projected climate change adds an additional layer of risk to these ecosystems that are already prone to land degradation due to mismanagement and growing population pressure. In general, effective adaptation to climate change in these sensitive ecosystems is limited by the availability of information on how to adapt. Therfore, so-called pre-meditated adaptation that begins with anticipation and information is an indispensable element of a comprehensive climate policy: Ecological expertise has to be transfered to farmers in order to help them to prepare for and cope with unavoided impacts of climate change.

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6 General Discussion

The need to develop sustainable resource management strategies for semi-arid and arid rangelands is acute as non-adapted grazing strategies lead to irreversible environmental problems such as desertification and associated loss of economic support to society. However, successful implementation of sustainable management for semi-arid and arid rangelands strategies depends on profound understanding of processes at different scales that underlay the complex system dynamic.

In this thesis I addressed two topics, both related to the question how to enhance sustainable management of semi-arid and arid rangelands: Firstly, I want to discuss one particular factor identified as being important for sustainable grazing management: the interaction of ecological and hydrological processes. Then, I want to point out a second central aspect of the study, this being the necessity of comprehensive understanding the interplay between human influence and ecosystem dynamics.

Therefore, I combined a range of integrative modelling approaches that help to assess potential future trends of these complex systems: I developed (i) a simulation model operating at small spatial scales to investigate the relative impact of small scale soil-plant interactions on vegetation dynamics, (ii) a simulation tool which has the power to transfer these small-scale processes to larger spatial scales and (iii) an integrated ecological-economic approach that consists of an ecological and an economic module and combines relevant processes on either level.

1. Ecohydrological processes at different spatial scales

Despite the awareness that particularly in arid and semi-arid regions ecological and hydrological processes interact, our knowledge on the strength and extent of the impact of geomorphology and landuse on vegetation and hydrological dynamics is still poor.

With the aid of a small-scaled and spatially-explicit simulation model I showed that ecohydrological interactions gain importance in particular in rangelands with ascending slope. In these systems vegetation cover serves to obstruct run-off and decreases evaporation from the soil. Disturbances like overgrazing influence these positive feedback mechanisms by affecting vegetation cover and composition.

However, run-off also occurs at large spatial scales (Rango et al. 2006). Until now, landcover change applications omit this process what directly affects the accuracy of predictions (Heuvelink 1998, Weaver and Perera 2004). Therefore, I constructed a modelling approach that has the power to transfer and integrate ecological information from the small scale vegetation model to the landscape scale which is most relevant for the conservation of biodiversity and sustainable management of natural resources. I combined techniques of stochastic modelling with remotely sensed data and

GIS to investigate to which extent spatial interactions, like the movement of surface water by run-off in water limited environments, affect ecosystem functioning at the landscape scale. My simulation experiments show that surface run-off increases biomass production at light grazing intensities. In contrast, overgrazing destabilizes positive feedbacks through vegetation and hydrology and decreases the number of hydrological sinks. The buffer capacity of these hydrological sinks disappears and run-off increases.

The investigation of the two studies leads to an improved understanding about the significance of soil-plant interactions in general. I recommend that different vegetation types should not only be regarded as provider of forage production but also as regulator of ecosystem functioning. In particular vegetation patches with good cover of perennial vegetation are capable to catch and conserve surface run-off from degraded surrounding areas. This consequence also applies to commercial rotational grazing strategies for semi-arid and arid rangelands with ascending slope. In general periodic resting is seen to prevent degradation (e.g. Heady 1999, Batabayal and Beladi 2002, Müller et al. 2007) thus enabling paddocks to act as hydrological sinks. Downstream out of the grazing system and artificial droughts are prevented, the system keeps its buffer capacity and efficient use of water resources is guaranteed.

2.   Complex interactions between land use and vegetation dynamics

By the help of an integrated ecological-economic modelling approach, I analyzed the relevance of the farmers' ecological knowledge for sustainable management and longterm functioning of semi-arid and arid grazing systems. A central result is that sustainable management of semi-arid and arid rangelands relies strongly on the farmers' knowledge on how the ecosystem works: In contrast to a farmer with perfect ecological knowledge, an optimistic farmer overestimates the positive effects of annual rainfall on vegetation dynamics. Particularly in years with low annual rainfall, he applies stocking rates that lead to vast degradation.

These results are in line with the assumption that a lack of knowledge is generally an obstacle for effective implementation of sustainable rangeland management (Buxton and Stafford Smith 1996, Janssen 2004, Quaas 2007). But mismanagement is not only a lack of knowledge, to which the answer would be either more research or better transfer of knowledge to rangeland managers. In many cases rangeland managers are insufficiently engaged to adopt even if adequate knowledge does exist as they behave to maximise their short-term profit (Carpenter and Gunderson 2001). Here, my simulation model serves as a tool that enables to explain the long-term consequences of different management decisions and can be of great help in an interactive process between researchers and stakeholders.

However, due to current and predicted future climate change, sustainable agriculture is not just a set of practices but a process requiring skills of adaptability (Wall and Smit 2005). The simulation results demonstrate that the projected lower annual rainfall due to climate change in combination with non-adapted grazing strategies adds an additional layer of risk to these ecosystems that are already prone to land degradation. By comparing different types of rangeland managers I showed that effective adaptation to climate change in these sensitive ecosystems is limited by the availability of information on how to adapt: Both, an inactive and a reactive manager are ill-prepared for future climatic conditions. The former through not expecting the system to change at all and the latter since the optimal reactive response is partially built around past experience. Only a proactive manager uses information about change, especially if the technical forecasts incorporate enough process understanding to remain correct each year as the climate changes. I conclude that so-called pre-meditated adaptation that begins with anticipation and information is an indispensable element of a comprehensive climate policy: Ecological expertise has to be transferred to farmers in order to help them to prepare for and cope with unavoidable impacts of climate change.

My study highlights that economic and environmental dimensions are inseparable within sustainable management, and each is equally critical: From an environmental perspective, human activities affect ecosystem dynamics. If the ecosystem is pushed too far, its integrity will be destroyed, ultimately leading to a decline in agricultural productivity. From a human point of view, sustainability describes the use of natural resources no faster than they can regenerate themselves. Economically unsustainable farms may loose control of their ecological resources.

However, one critical assumption about my ecological-economic modelling approach is that the economic module is based on a linear optimization model: Such optimization models generally assume that the virtual rangeland manager maximises his net income over a specified time based on his constant understanding of the system dynamics (e.g. Perrings and Walker 1997, Batabyal 1999, van Wenum et al 2004). In contrast, real resource management systems are rather dynamic and can be looked upon as natural experiments that are experiential through learning-by-doing (e.g. Carpenter et al., 1999, Jannsen et al. 2000, Olsson and Folke 2001, Carpenter et al. 2005).
Nevertheless, my ecological-economic modelling approach fulfills the requirements as it was not aimed to simulate reality but to make the complex system dynamics understandable and to demonstrate the importance of adaptation to climate change. In general, such models that help to enhance the mechanistic understanding of processes are seen as a crucial precondition for making predictions (Levin 1992).

3.   Outlook

This thesis showed that an understanding of the interaction of different disciplines and spatial scales has important implications for improving sustainable management of semi-arid and arid rangelands. All simulation models focus on the most essential factors and ignore specific details. Therefore, even though all simulation models are parameterized for a specific dwarf shrub savannah in arid southern Namibia, the conclusions drawn are applicable for semi-arid and arid rangelands in general.

The next step for a multidisciplinary environmental assessment would be the linkage of relevant ecological and economic processes at a regional scale. The basis for this extension could be based on my upscaling method but requires a combination of spatial economics and landscape ecology. Integration of both disciplines into a simulation model needs to cover geomorphological heterogeneity of the landscape as well as regional and transport economics which deal with local decisions of households, land allocation, spatial markets and interregional flows of products, capital and labour as well as interregional externalities.

This approach will allow for a detailed investigation on how not only climatic but also demographic and global economic changes affect the applicability of sustainable management strategies.

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7 Zusammenfassung

Nachhaltige Mangementstrategien für semi-aride und aride Beweidungsgebiete sind äusserst bedeutend, da ein nicht nachhaltiges Management in diesen Gebieten zu irreversiblen Umweltproblemen wie Desertifikation und damit verbundenem Verlust der ökonomischen Prosperität führt. Für eine erfolgreiche Entwicklung nachhaltiger Strategien in derart gefährdeten Ökosystemen ist ein fundiertes Verständnis der ökologischen Prozesse auf verschiedenen räumlichen Skalen grundlegend.

Obwohl Wasserverfügbarkeit und Viehmanagement als die bedeutendsten Faktoren für die Dynamik semi-arider und arider Ökosysteme angesehen werden, ist die Interaktion von ökologischen und hydrologischen Prozessen nicht genügend erforscht. Ausserdem werden in den meisten Forschungsarbeiten sowohl der menschliche Einfluss auf, als auch dessen Abhängigkeit von Ökosystemdynamiken nicht berücksichtigt.

Um grundsätzliche Richtlinien für die nachhaltige Nutzung semi-arider und arider Beweidungsgebiete zu erstellen, habe ich in dieser Arbeit mehrere Modellierungstechniken miteinander kombiniert. Mit dieser Herangehensweise lassen sich sowohl verschiedene Wissenschaftsdisziplinen als auch räumliche Skalen integrieren.

Meine Arbeit besteht aus drei Teilen, die aufeinander aufbauen.

Für den ersten Teil meiner Arbeit habe ich ein gitterbasiertes und kleinskaliges Modell entwickelt, welches die Vegetationsdynamik und die damit verbunden hydrologischen Prozesse simuliert. Die Simulationsergebnisse zeigen, dass öko-hydrologische Interaktionen in Beweidungsgebieten mit ausgeprägter Topographie durchaus von Bedeutung sind: Eine dichte Vegetationsbedeckung kann Oberflächenwasserabfluss aufhalten und Evaporation aus dem Boden reduzieren. Störungen wie Überweidung beeinflussen diesen positiven Rückkopplungsmechanismus negativ, indem sie Vegetationsbedeckung und -zusammensetzung verändern.

Im zweiten Teil der Arbeit stelle ich eine Methode vor, mit deren Hilfe man diese kleinskaligen ökologischen Informationen auf die Landschaftsebene übertragen kann. Dies ist von grundlegender Bedeutung, da Entscheidungen bezüglich des Schutzes von Biodiversität als auch zur nachhaltigen Nutzung von Resourcen auf der Landschaftsebene getroffen werden müssen. Hier habe ich Techniken der stochastischen Modellierung mit Techniken der Fernerkundung und GIS kombiniert, um zu untersuchen wie räumliche Interaktionen (in diesem Falle Oberflächenabfluss) das Funktionieren von Ökosystemen auf Landschaftsebene beeinflussen. Meine Simulationsergebnisse zeigen, dass Überweidung die Anzahl an Vegetations-Patches, die als hydrologische Senken fungieren, reduziert und somit der Oberflächenabfluss ansteigt.

Die Ergebnisse beider Simulationsmodelle implizieren, dass die verschiedenen Vegetationstypen nicht nur als Futterquelle für die Weidetiere betrachtet werden sollten, sondern auch bezüglich ihrer Bedeutung als Regler der Ökosystemfunktion. Vegetations-Patches mit einem hohen Bedeckungsgrad an perennierender Vegetation können Oberflächenabfluss aus degradierten benachbarten Gebieten abfangen. Somit ist eine effiziente Nutzung der Wasserresource garantiert. Meine Ergebnisse haben deshalb auch Bedeutung für die kommerzielle Rotationsbeweidung in ariden und semi-ariden Gebieten mit ausgeprägter Topographie, wo nicht-degradierte Koppeln als hydrologische Senken fungieren können.

Im letzten Teil der Arbeit habe ich mit Hilfe eines integrierten ökologisch-ökonomischen Simulationsmodells die Bedeutung des ökologischen Verständnisses der Farmer für ein langfristiges Funktionieren von semi-ariden und ariden Beweidungssystemen unter aktuellen und prognostizierten klimatischen Bedingungen untersucht. Der Modellansatz besteht aus einem ökologischen sowie einem ökonomischen Modul und kombiniert die relevanten Prozesse auf beiden Ebenen. Auch hier wird die Vegetationsdynamik und – produktivität beider Module mit Hilfe des kleinskaligen Vegetationsmodells abgeleitet. Die Ergebnisse zeigen, dass ein nachhaltiges Management semi-arider und arider Savannen sehr stark vom Verständnis der Farmer für die Funktionsweise des Ökosystems abhängt. Des Weiteren weisen meine Simulationsergebnisse darauf hin, dass ein durch den prognostizierten Klimawandel reduzierter Jahresniederschlag in Kombination mit nicht-angepassten Beweidungsstrategien ein weiteres Risiko für diese Ökosysteme bedeutet, die schon heute durch Degradation bedroht sind.

Meine Arbeit trägt zu einem besseren Verständnis grundlegender Prozesse der Ökosystemdynamik einer ariden Zwergstrauchsavanne im südlichen Namibia bei. Da sich alle drei Simulationsmodelle auf grundlegende Faktoren konzentrieren und spezifische Details ignorieren, können die Schlussfolgerungen auch auf andere semi-aride und aride Beweidungsgebiete übertragen werden.

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