

Shifting thresholds and changing degradation patterns: climate change effects on the simulated long-term response of a semi-arid savanna to grazing

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Summary

1. The complex, nonlinear response of dryland systems to grazing and climatic variations is a challenge to management of these lands. Predicted climatic changes will impact the desertification of drylands under domestic livestock production. Consequently, there is an urgent need to understand the response of drylands to grazing under climate change.

2. We enhanced and parameterized an ecohydrological savanna model to assess the impacts of a range of climate change scenarios on the response of a semi-arid African savanna to grazing. We focused on the effects of temperature and CO₂ level increase in combination with changes in inter- and intra-annual precipitation patterns on the long-term dynamics of three major plant functional types.

3. We found that the capacity of the savanna to sustain livestock grazing was strongly influenced by climate change. Increased mean annual precipitation and changes in intra-annual precipitation pattern have the potential to slightly increase carrying capacities of the system. In contrast, decreased precipitation, higher interannual variation and temperature increase are leading to a severe decline of carrying capacities owing to losses of the perennial grass biomass.

4. Semi-arid rangelands will be at lower risk of shrub encroachment and encroachment will be less intense under future climatic conditions. This finding holds in spite of elevated levels of atmospheric CO₂ and irrespective of changes in precipitation pattern, because of the drought sensitivity of germination and establishment of encroaching species.

5. *Synthesis and applications.* Changes in livestock carrying capacities, both positive and negative, mainly depend on the highly uncertain future rainfall conditions. However, independent of the specific changes, shrub encroachment becomes less likely and in many cases less severe. Thus, managers of semi-arid rangelands should shift their focus from woody vegetation towards perennial grass species as indicators for rangeland degradation. Furthermore, the resulting reduced competition from woody vegetation has the potential to facilitate ecosystem restoration measures such as re-introduction of desirable plant species that are only little promising or infeasible under current climatic conditions. On a global scale, the reductions in standing biomass resulting from altered degradation dynamics of semi-arid rangelands can have negative impacts on carbon sequestration.

Key-words: CO₂ increase, demographic bottleneck, ecohydrology, grid-based simulation model, livestock, precipitation pattern, savanna resilience, shrub encroachment, soil moisture, sustainable rangeland management

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Introduction

Dry rangelands world-wide are prone to concurrent high levels of human intervention and high climatic variability (Gillson & Hoffman 2007; Reynolds *et al.* 2007). The consequence is often desertification, that is, a decrease in vegetation cover and/or a change of vegetation composition with a subsequent loss of the systems productivity (UNCCD 1994). In many regions, land use intensities are expected to further increase because of global population growth, leading to even higher stress levels in rangeland systems (UNCCD 1994; Reynolds *et al.* 2007). At the same time, water availability is likely to be altered as a result of the predicted temperature increase and changes in precipitation amount and variability (IPCC 2007; Scheiter & Higgins 2009). Thus, two of the most important external drivers of dryland ecosystems, climate and land use, are likely to change simultaneously. An understanding of the underlying mechanisms of dryland dynamics and the drylands' response to predicted changes is of utmost importance (Tietjen & Jeltsch 2007).

Many studies agree that dryland systems such as semi-arid savannas are not at equilibrium, but are driven by stochasticity and variability in environmental drivers such as precipitation, fire and herbivory (Fensham, Fairfax & Archer 2005; Gillson & Hoffman 2007). In their response to land use, semi-arid savannas can exhibit pronounced thresholds, and consequently, degradation processes are nonlinear and difficult to anticipate (Jeltsch, Weber & Grimm 2000; Vetter 2005; Gillson & Hoffman 2007).

Conceptual models addressing the mechanisms behind the coexistence of grasses and woody vegetation have focussed on either competitive interactions between trees and grasses or the demographic bottlenecks related to tree establishment (Sankaran, Ratnam & Hanan 2004). Recently, it was suggested that both mechanisms play an important role on different levels or scales of the system (Sankaran, Ratnam & Hanan 2004; Meyer, Wiegand & Ward 2009). However, both competitive and demographic processes are influenced by the two central drivers of the system, namely land use and climatic variability.

In particular, livestock grazing influences both competitive interactions between grasses and woody species as well as woody species recruitment. Herbivores were found to increase the recruitment success of many encroaching species by enhancing tree seed dispersal and by increasing germination rates after ungulate gut passage of the seeds (Miller 1995; Tews, Schurr & Jeltsch 2004). More importantly, the selective removal of grass biomass leads to reduced competition from grasses, resulting in an increased establishment rate of shrubs (Kraaij & Ward 2006; Hiernaux *et al.* 2009; Ward & Esler 2011).

The influence of variability in precipitation is dependent on the temporal scale that is considered. On an intra-annual scale, the timing of precipitation can be crucial for plant phenology. The size of precipitation events has a strong impact on available soil moisture and related processes such as growth, mortality or establishment (see pulse theory: Schwinning & Sala 2004): on the one hand, sufficiently large

precipitation events are needed in order to obtain deep infiltration and thus less losses through evaporation; on the other hand, intense rainfall events can lead to high water losses through run-off if the soil texture, structure and roughness do not allow for fast infiltration (Fensham, Fairfax & Archer 2005; Tietjen, Zehe & Jeltsch 2009; Tietjen *et al.* 2010). Variations in the interannual scale increase the frequency of multiyear droughts and can therefore cause severe diebacks of grasses. Juvenile shrubs and seedlings with low competitive strength especially benefit from such situations (Buitenwerf, Swemmer & Peel 2011; Ward & Esler 2011). Additionally, interannual variation causes consecutive years with above-average precipitation which enable episodic mass recruitment of woody species (Kraaij & Ward 2006; Joubert, Rothauge & Smit 2008).

Inter- and intra-annual precipitation patterns are predicted to change in semi-arid and arid environments in the course of climate change, leading to an increased number of extreme events (IPCC 2007). Furthermore, predictions include increases in mean temperature and atmospheric CO₂ levels as well as changes in mean annual precipitation (MAP) for many dry regions (IPCC 2007). Unfortunately, climate model predictions are subject to high uncertainty; therefore, the direction of change can vary between different climate models (IPCC 2007). Increased evaporation and transpiration rates will lead to decreased water availability. Negative and positive changes in MAP can mitigate or exacerbate these effects, respectively. The water use efficiency in turn can be positively influenced by increased levels of atmospheric CO₂ (Drake, González-Meler & Long 1997; Scott *et al.* 2006), which potentially favours woody vegetation over grasses owing to their different carbon pathways (Bond, Midgley & Woodward 2003; Kgope, Bond & Midgley 2010).

In order to systematically analyse the influence of a realistic range of possible climatic changes on the response of a dryland ecosystem to land use, we exemplarily address degradation in an African camelthorn savanna. In such semi-arid savannas, degradation in general was found to occur when certain long-term grazing intensities have been exceeded (Weber & Jeltsch 2000; Joubert, Rothauge & Smit 2008). In most cases, the degradation pattern was shrub encroachment, where perennial grass abundance is decreased and woody plant species become dominant (e.g. Skarpe 1990). The consequence is a decrease in productivity and biodiversity of the system (Blaum *et al.* 2009).

We assessed savanna rangeland response for a broad range of grazing intensities and climate change scenarios applying a modified ecohydrological model (Tietjen *et al.* 2010). We simulated changes in intra- and interannual patterns of precipitation as well as modifications of long-term means. Further, we assessed the effects of an increase in the atmospheric CO₂ level and mean temperature.

In particular, we address the following questions: (i) How do changes in different climate patterns impact the long-term threshold of livestock density up to which a savanna persists in a non-degraded state and what are their combined effects? (ii) If degradation occurs, does the

pattern of degradation in terms of relative and absolute abundance of shrubs, perennial and annual grasses differ between the different climate change scenarios?

Materials and methods

STUDY AREA

The model was applied to a Namibian Acacia-tree-and-shrub savanna of the Central Kalahari type (Mendelsohn *et al.* 2002) as it is found at the governmental research station at Sandveld (latitude 22°02'S, longitude 19°07'E). This area was used for livestock production for about 80 years and has been a research farm since the late 1960s. It is considered a typical shrub-encroached savanna that is invaded by *Acacia mellifera* BENTH., although the level of degradation is still considered to be moderate.

Precipitation falls during summer months (September to April) and has a high inter- and intra-annual variation. The MAP measured at Sandveld during 23 years (1986–2008) was 408 mm with a standard deviation of 180 mm (Rothauge 2006). The annual mean temperature is about 19 °C, with monthly means ranging from 12 °C (July) to 25 °C (January). The area is characterized by loamy Kalahari sand soils. The topography of the area is very flat with a mean height of 1520 m.

MODEL DESCRIPTION

Our model is based on the grid-based ecohydrological dryland model *EcoHyD* (Tietjen *et al.* 2010). It is a combination of a process-based savanna vegetation submodel calculating the biweekly growth of two plant functional types (shrubs and perennial grasses) and a process-based hydrological submodel, calculating daily moisture dynamics in two soil layers (Tietjen, Zehe & Jeltsch 2009) for 30 × 30 grid cells each representing 5 × 5 m² patches resulting in a total simulated area of 2.25 ha. No changes have been made to the hydrological submodel, but the vegetation model was modified to address land use-related questions.

The vegetation submodel comprises the processes growth, mortality (induced by drought or senescence), competition for water and space, dispersal and establishment for shrubs, perennial grasses and annuals. In addition to the model described by Tietjen *et al.* (2010), we introduced a grazing/browsing algorithm, and the algorithms for dispersal and establishment were changed to account for grazing effects. We included annual grasses as a third functional type in addition to perennial grasses and woody vegetation, because annual vegetation may contribute considerably to the diet of livestock (Tainton 1999; Rothauge 2006). We furthermore changed the rules for establishment and mortality of the woody vegetation, taking into account the ecology of the dominant encroacher species in the study area, that is, *A. mellifera*.

A comprehensive description of the model rules can be found in Appendix S1 (Supporting information). All simulations were conducted using the parameter set given in Tables S1 and S2 (Supporting information).

SIMULATIONS

In this study, we applied a full-factorial design, to simulate all possible combinations of the implemented levels of land use intensity, precipitation pattern, temperature and atmospheric CO₂.

Unless otherwise noted, all results are based on 25 repeated simulations of 200 years, each with unique time series of stochastic

precipitation and temperature according to the respective climate scenario (see below).

Initial grass cover was randomly drawn from a uniform distribution with values of perennial grass canopy cover between 40% and 80% per cell. Shrub canopy cover was randomly distributed in 20% of all cells with values of 1–80% per cell. In cells with woody vegetation, initial grass cover was limited to 5%.

A model spin-up was performed for each simulation for 50 years with the respective climate scenario and without livestock grazing, to allow for the system to reach a steady state before testing management scenarios.

Land use

Land use scenarios were implemented as different densities of livestock that were kept constant over time. Scenarios range from 3.3 large stock units (LSU) per 100 hectares to 10 LSU 100 ha⁻¹ plus an additional scenario representing no grazing by livestock. We use the definition of a LSU as a 450-kg live weight cattle (Meissner 1982). Natural grazing and browsing of game are not simulated but are implicitly included because the presence of game presumably influenced all data that were used for model parameterization.

Precipitation pattern

We generated precipitation and temperature time series with hourly resolution as described in the study by Tietjen *et al.* (2010). The derived time series showed no significant difference in mean value, distribution and variance compared to measured annual precipitation in Sandveld during 1983–2007.

We implemented three types of changes in precipitation patterns following the range of possible changes given by the global climate models (GCMs) in the IPCC report (2007) and available studies of regional climate models (RCMs) for southern Africa (Tadross, Jack & Hewitson 2005; Engelbrecht, McGregor & Engelbrecht 2009): (i) change of MAP by ± 10% (as GCMs and RCMs disagree on the sign of changes). For this, the size of all generated rainfall events was changed by ± 10%, respectively. (ii) A change in the intra-annual distribution of precipitation towards more large events and less small events. This was generated by shifting the total precipitation amount of events falling into the lowest quantile (10%) to precipitation events falling into the upper 90% quantile while keeping the MAP fixed (as given in Tietjen *et al.* 2010). (iii) Change in the interannual distribution of precipitation towards an increased probability of above-average (> 500 mm) and below-average (< 300 mm) precipitation years. For this, we reshaped the probability distribution of annual precipitation (clustered in 100 mm classes) by reducing probabilities of the two precipitation classes embracing the MAP (300–400 mm and 400–500 mm). The subtracted probability was added to below-average and above-average precipitation classes, respectively, revealing a new, stretched distribution with an unchanged median. This increased the coefficient of variation of annual precipitation by 0.1–0.45.

In addition, all possible combinations of these three changes were implemented.

Temperature and CO₂

Our temperature and CO₂ scenarios are based on the climate change scenarios for 2080–2099 given by the A1B scenario of the IPCC (2007) report. This includes an increase in annual mean temperature by 3.5 °C and increased atmospheric CO₂ levels up to 700 ppm.

The effect of increased CO₂ levels on the system is regarded in two ways. Following the implementation of Tietjen *et al.* (2010) that is based on free-air CO₂ enrichment experiments (Ainsworth & Long 2005), we decreased transpiration from the lower soil layer by 40% and secondly increased the potential growth rates of plants. The latter was found to be stronger for plants using a C₃ pathway for carbon fixation in photosynthesis than for the C₄ pathway, because C₄ photosynthesis is often saturated or nearly saturated under ambient conditions (Morgan *et al.* 2004). As most grasses in tropical savannas feature C₄ pathways (Polley 1997), we assume that CO₂ enrichment leads to an increase in potential growth rate of grasses by 30% and potential growth rate of shrubs by 90% according to Bond, Midgley & Woodward (2003). Note that these rates are potential growth rates, and growth is additionally strongly limited by water availability and competition.

Sensitivity analysis and validation

In order to improve confidence in simulation results, we conducted a sensitivity analyses by varying all parameters by $\pm 10\%$ and $\pm 20\%$. The model output was furthermore validated against three empirical patterns (relation of annual precipitation to grass biomass production of African savannas, shrub cover and biomass production of the study site). Details of these analyses can be found in Appendix S2 (Supporting information).

Results

PRESENT DYNAMICS AND EFFECTS OF LIVESTOCK GRAZING

Under present climatic conditions, the simulations without livestock grazing lead to a savanna system that is in a stable state, with especially the annual and perennial grasses strongly responding to fluctuations in the highly variable precipitation (Fig. 1a). Perennial grass cover is high (mean value: 65%, SD: 11.3), while shrub cover and annual grass cover are low (mean values: 8%, SD: 1.2 and 7%, SD: 3.2, respectively), leading to a dense grass matrix with sparse shrubs. Continuous high grazing, however, deteriorates the system and drives it to another dynamic state (Fig. 1b) that is dominated by high levels of shrub cover (mean value 29%, SD: 8.5), while perennial grasses are nearly absent (mean value <1%). In this shrub-encroached state, annual grasses vary strongly with precipita-

tion and reach much higher maximum values of cover than in scenarios without livestock grazing (mean value 19%, SD: 7.7).

In general, the perennial grass matrix is severely threatened by rarely occurring severe droughts or series of years with below-average precipitation (e.g. Fig. 1a years 26–27). If grazing pressure is high in addition to such drought events, this might lead to a complete loss of perennial grasses (see Fig. 1b, year 40). However, the loss of perennial grasses does not immediately lead to shrub encroachment, but causes an interim state dominated by annual grasses (see Fig. 1b, years 50 et seq.). If a series of above-average precipitation years occurs during this state, events of major shrub establishment success can lead to a shrub-encroached system (see Fig. 1b, years 67–68 and 173–174). Once the shrubs are established, their cover varies over time as a result of age- and drought-dependent mortality.

EFFECTS OF CLIMATE CHANGE

The simulated scenarios show that climate change will have strong direct and indirect effects on soil moisture. All scenarios lead to decreased mean soil moisture content of the upper soil layer, whereas the change in moisture content of the lower layer shows no consistent trend, but depends on the respective precipitation pattern (Fig. 2). Compared to current climatic conditions (scenario c), both the moisture in the upper layer and that in the lower layer are decreased by simultaneous increases in temperature and CO₂ (scenario p). If, in addition to increased temperature and CO₂, precipitation falls in fewer, but larger events (scenario s) or if MAP is increased (scenario +10), soil moisture in the lower layer increases. In contrast, a reduced MAP (scenario-10) leads to a decreased lower-layer soil moisture.

Furthermore, altered climatic conditions impact vegetation cover (Fig. 3). Perennial grass cover increases with an increase in size of large precipitation events (s) or in MAP (+10) and is reduced when both a decrease in MAP and increased interannual variation in precipitation are assumed (v-10). The pattern is very similar for shrubs, although relative differences between the simulated scenarios are much more pronounced. An increase in size of large events (s) and an increased MAP (+10) have positive implications for the abundance of shrubs, also

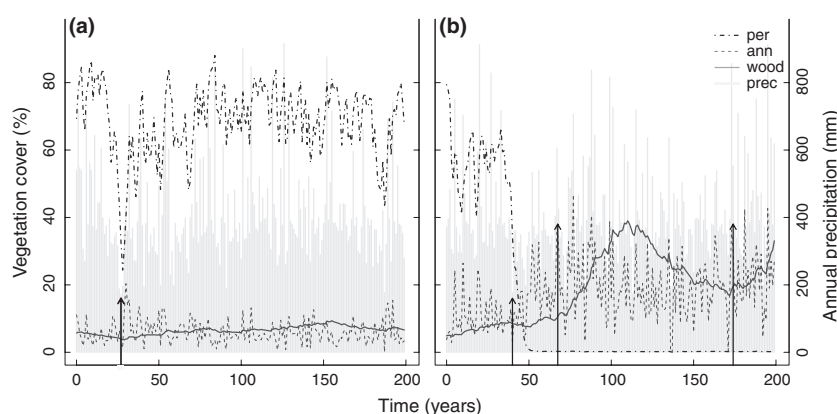


Fig. 1. Time series of mean vegetation cover (%) and respective annual precipitation (mm) for showcase single runs of 200 years for simulations (a) without livestock grazing and (b) with intense livestock grazing [8.3 large stock units (LSU) 100 ha⁻¹]. Arrows indicate examples of precipitation events causing grass collapse or shrub recruitment.

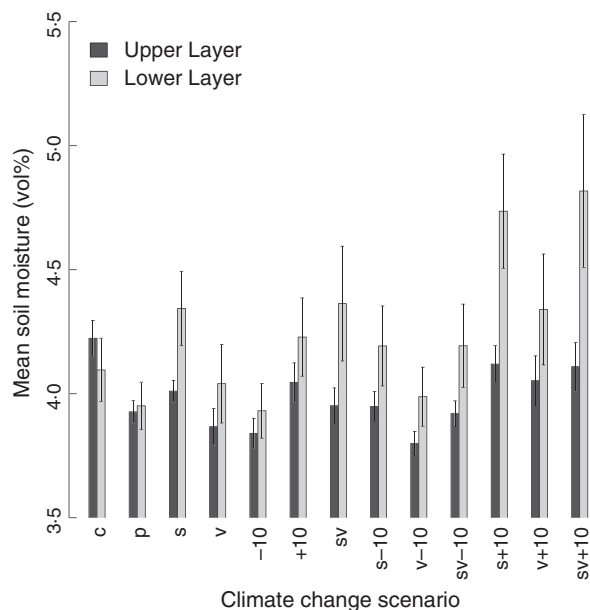


Fig. 2. Mean and standard error of 25 replicate simulations of initial soil moisture ($t = 10$) during the growing season in upper and lower layers without livestock grazing (see Table 1 for scenario description). Scenario c shows results for the scenario with current climatic conditions.

when combined with increased interannual variation. Scenarios of reduced MAP (–10) lead to decreased shrub cover, while an increase in interannual variation (v) has no clear effects.

Compared to these effects of altered precipitation patterns, the effects of increased CO₂ levels on shrub and perennial grass cover are moderate. Grasses tend to slightly benefit from increased CO₂ for all precipitation scenarios, while shrubs show no pronounced or clear response, especially because they are limited by competitive interactions with dominant perennial grasses. In contrast, increased mean annual temperature has a pronounced negative impact on both shrub and perennial grass cover in all precipitation scenarios. Consequently, the concurrent effects of CO₂ level and temperature increase are dominated by the unambiguously stronger temperature effects, thus resulting in decreased values of shrub as well as perennial grass cover compared to the respective reference scenario (i.e. the same precipitation pattern).

To further evaluate the importance of water availability in the upper soil layer and related germination and early establishment of shrubs for long-term vegetation effects, we compared initial mean soil moisture with final shrub cover of simulations under high livestock grazing intensities (Fig. 4). As we are interested in the cause of final vegetation pattern rather than its feedback on soil moisture, we use initial soil moisture values (mean of 25 replicates at $t = 10$) for this correlation. Interestingly, initial soil moisture in the upper layer and final shrub cover show a clear correlation ($R^2 = 0.59$; $P < 0.01$). In contrast, the correlation of final shrub cover with lower-layer soil moisture was not significant ($R^2 = 0.11$; $P = 0.27$). Grasses were similarly linked to moisture in both layers ($R^2 = 0.55$ and $R^2 = 0.78$ respectively $P < 0.001$).

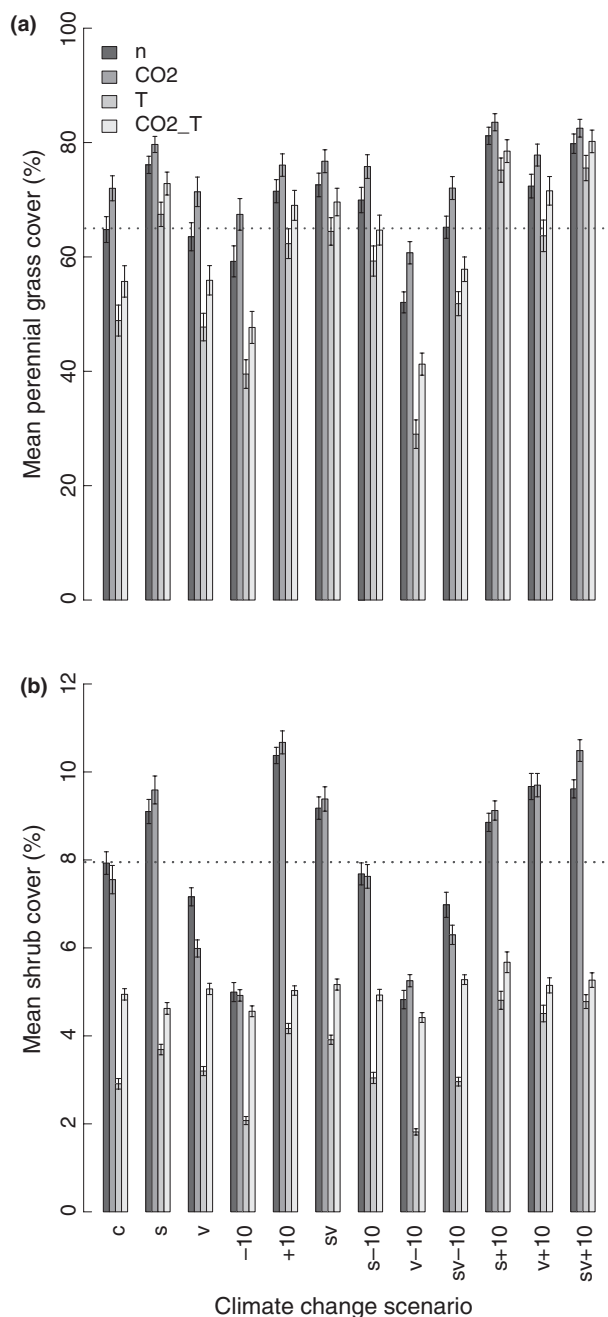


Fig. 3. Mean and standard error of final cover of (a) perennial grasses and (b) woody vegetation for different precipitation scenarios (see Table 1) from 25 repeated simulations of 200 years without grazing; different bars depict results for simulations with no changes (n) or singular increase in either mean annual temperature (T) or CO₂ levels (CO₂) or an increased level of both at a time (CO₂_T); the dashed line delineates cover resulting from simulations of current climatic conditions.

COMBINED EFFECTS OF CLIMATE CHANGE AND LAND USE

In general, the response of the system to grazing follows a threshold behaviour regarding grazing intensity: under current climatic conditions, the system remains in its original state with

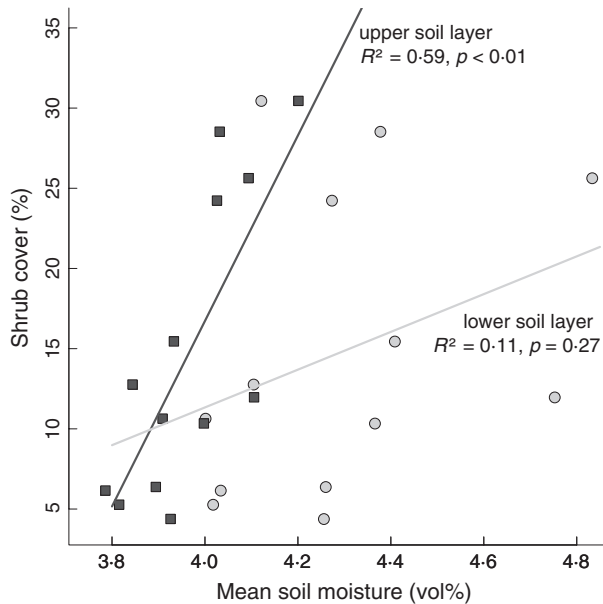


Fig. 4. Final mean values of shrub cover ($t = 200$) and regression dependent on initial mean soil moisture ($t = 10$) derived from 25 simulations with intense livestock grazing [8.3 large stock units (LSU) 100 ha^{-1}] for all 13 climate scenarios. Squares show data for upper soil layer and circles for lower soil layer.

stocking rates up to about $6 \text{ LSU } 100 \text{ ha}^{-1}$ (Fig. 5). If grazing intensity increases, the probability of degradation towards an increased level of shrubs and annuals and a decreased level of perennial grasses increases rapidly (Fig. 5, compare also with single runs in Fig. 1).

This response of the system to livestock grazing can be altered substantially by the simulated climate change scenarios

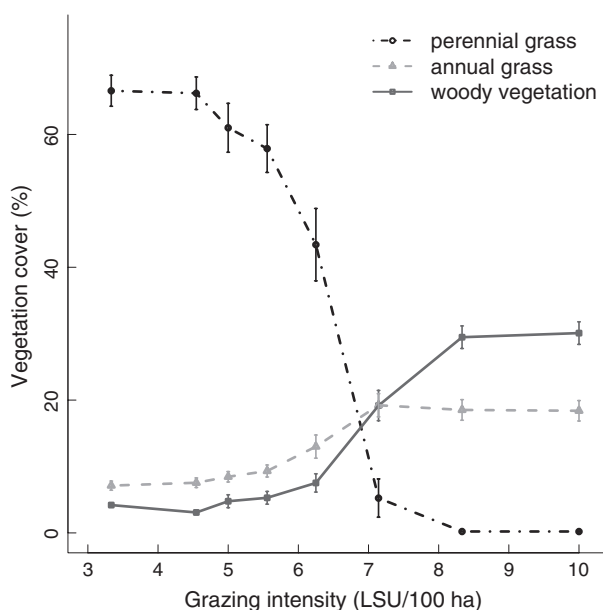


Fig. 5. Mean and standard error of final cover of perennial and annual grasses and shrubs at different livestock densities. Results were derived from 25 repeated simulations of 200 years under current climatic conditions.

(Fig. 6a–l) with respect to both the collapse of the perennial grass matrix and the encroachment of shrubs.

The productivity of perennial grasses and hence the grazing resistance of the system (i.e. the grazing threshold where degradation occurs) are reduced by the simulated increase in temperature (Fig. 6e). This situation is worsened compared to current climate conditions if the interannual variability of precipitation is increased (Fig. 6g) or MAP is decreased (Fig. 6a) or both (Fig. 6c). However, negative effects of temperature increase can be compensated by the positive effects of an increased MAP (Fig. 6i) or increased intra-annual variation in precipitation leading to more large, and thus effective, precipitation events (Fig. 6f). A combination of such changes even leads to increased grass cover despite the negative effects of increased temperature (Fig. 6j). In general, annual grass cover is negatively related to perennial grass cover and therefore increases with higher livestock grazing intensity.

The response of woody vegetation to land use is also influenced by climate change. As described above, maximum shrub cover values under high grazing pressure are often reduced drastically if the mean water content of the upper soil layer is decreased (Fig. 4). While a high grazing intensity leads to shrub encroachment, under present climatic conditions (Fig. 5), climate change scenarios that reduce upper soil moisture levels lead to the dominance of annual vegetation or increased bare ground instead of increased shrub cover (Fig. 6a–h). The level of shrub encroachment resulting from grazing is highly dependent on MAP: if, in addition to higher temperatures and increased CO_2 levels, MAP decreases by 10%, none of the changes in the intra- or interannual rainfall distribution leads to shrub encroachment. If MAP remains the same, we see slight shrub encroachment if grazing intensity increases, but annual vegetation dominates the system. In contrast, high grazing in combination with an increase in MAP by 10% is leading to shrub dominance on levels that are similar to encroachment under current climatic conditions (Fig. 6i–l).

Discussion

Following the state-and-transition concept (Westoby, Walker & Noy-Meir 1989), environmental drivers and land use can cause semi-arid savannas to switch between several possible vegetation states. These can broadly be categorized into a productive and desirable (e.g. in terms of livestock production or biodiversity) grass-dominated state and several degraded states dominated by annual vegetation, woody vegetation or bare ground (Westoby, Walker & Noy-Meir 1989; Reynolds *et al.* 2007). In this study, we successfully refined and applied a process-based ecohydrological model (Tietjen *et al.* 2010) to assess the impact of specific patterns of climate change on the response of a semi-arid savanna to land use. We found that the capacity of the system to sustain long-term livestock grazing is strongly influenced by most of the simulated climate change scenarios. Furthermore, our findings suggest that shrub encroachment, currently one of the major problems in the management of semi-arid rangelands, will be reduced under predicted future climatic conditions.

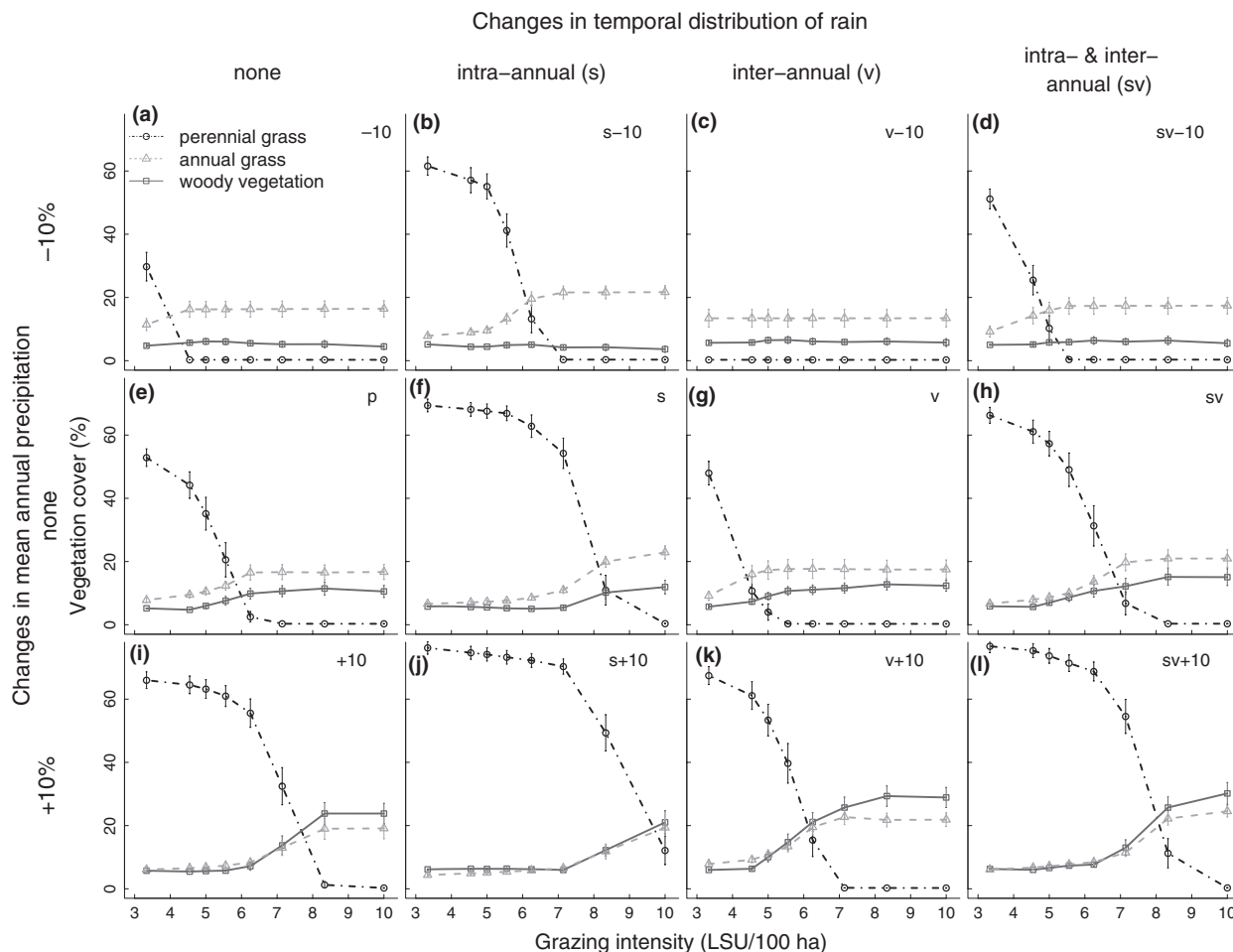


Fig. 6. Mean and standard error of final cover of perennial and annual grasses and shrubs at different livestock densities. Results were derived from 25 repeated simulations of 200 years under 12 different climate change scenarios comprising all combinations of changes in mean annual precipitation with changes in temporal distribution of rain. All simulations include an increase in mean temperature and atmospheric CO₂ as given by the A1B scenario of the 2007 IPCC report.

In the following, we discuss (i) the threshold of grazing intensity at which a transition between a non-degraded and a degraded state occurs and (ii) how the pattern of degradation, that is, the composition of vegetation types of the degraded system, may be influenced by climate change and (iii) the implications for the management of semi-arid rangelands.

SHIFTING THRESHOLDS

Perennial grass biomass is one of the most important factors for livestock production in drylands. Various studies have shown that perennial grass dynamics are mainly driven by the highly variable water availability, while grazing increases the resulting fluctuations in grass abundance (Fynn & O'Connor 2000; Weber & Jeltsch 2000; Buitenwerf, Swemmer & Peel 2011): if water availability decreases because of changes in climatic conditions, growth decreases and drought-induced mortality increases. This can even cause a collapse of the perennial grass matrix (Tietjen *et al.* 2010). If, in contrast, climate change leads to an increase in water availability (i.e. owing to changes in intra-annual distribution of precipitation or increased MAP), the perennial grass abundance becomes more stable. In

a nutshell, our study shows a shift in the threshold of grazing intensity, at which the system changes from a state dominated by perennial grasses to a state where plant types take over that are less suitable for livestock grazing or where vegetation cover is generally reduced.

Hereby, as also shown by our ecohydrological approach, changes in the intra-annual pulse size of precipitation events play a key role and have the potential to counteract the negative impacts of increased temperature and decreased MAP (Schwinning & Sala 2004). Dependent on soil texture and topography, an increased size of larger precipitation events at the cost of small events can cause a higher rate of water recharge of deeper soil layers (Reynolds *et al.* 2004; Schwinning & Sala 2004; Tietjen, Zehe & Jeltsch 2009) and consequently increased total water availability for plant growth. However, the shift of grazing thresholds that we found is to some extent site specific, because different soil types, soil crusts or slopes can cause limitations in the infiltration speed or changes in top-soil run-off (Tietjen, Zehe & Jeltsch 2009). Furthermore, this shift could potentially be mitigated if stocking rates are dynamically adapted (e.g. to available fodder) instead of keeping them constant over time.

Table 1. Climate scenarios and respective combinations of simulated changes in precipitation pattern

Scenario name	Changes in precipitation pattern			
	±10% MAP (±10)	Increase in size of large rainfall events (s)	Increase in interannual variation (v)	Increased Temperature & CO ₂
c	–	–	–	–
p	–	–	–	+
s	–	+	–	+
v	–	–	+	+
–10	–10	–	–	+
+10	+10	–	–	+
sv	–	+	+	+
s–10	–10	+	–	+
v–10	–10	–	+	+
sv–10	–10	+	+	+
s+10	+10	+	–	+
v+10	+10	–	+	+
sv+10	+10	+	+	+

MAP, mean annual precipitation.

Scenario c represents simulations with current climatic conditions (control).

CHANGING DEGRADATION PATTERN

Degradation of dryland savannas typically shows one of the following general patterns, mainly depending on the precipitation received: either vegetation composition changes, leading to shrub encroachment (Skarpe 1990; Wiegand, Ward & Saltz 2005; Graz 2008), or vegetation cover in general is drastically reduced and the fraction of bare ground is increased with temporarily dominating annual grasses (Jeltsch *et al.* 1997).

Our results indicate that if water availability decreases because of increased temperature or decreased MAP, woody vegetation will not be the dominant vegetation type in the degraded system state as under present climate conditions for this semi-arid savanna. The degradation pattern is instead driven towards a pattern typically found for more xeric savannas under current climatic conditions. But even for scenarios with increased MAP, shrub encroachment does not increase above the level that is found under current climatic conditions. This is particularly interesting, because several studies predict the opposite, that is, an increase in shrub encroachment owing to climate change despite temperature changes (Bond, Midgley & Woodward 2003; Kgope, Bond & Midgley 2010; Tietjen *et al.* 2010), which we did not find for any of our scenarios. Such conclusions are based on the fact that woody plant species, which follow the C₃ photosynthetic pathway, generally benefit more from elevated CO₂ levels than perennial grasses following the C₄ pathway (Bond, Midgley & Woodward 2003; Morgan *et al.* 2004). However, these studies either neglect the establishment bottleneck of woody savanna species (Tietjen *et al.* 2010), which was found in a wide range of empirical and theoretical studies (e.g. Sankaran, Ratnam & Hanan 2004; Joubert, Rothauge & Smit 2008; Meyer, Wiegand & Ward 2009), or they refer to more mesic conditions (Bond, Midgley & Woodward 2003; Kgope, Bond & Midgley 2010). In such mesic

savannas, water availability is higher and consequently germination and early stages of establishment of woody vegetation are rather occurring continuously over time, thus being less important for degradation dynamics. In fact, fires play a central role in such systems by controlling woody vegetation (Bond, Midgley & Woodward 2003). Consequently, direct effects of CO₂, like the increased growth rates, could be beneficial by increasing post-fire re-growth (Kgope, Bond & Midgley 2010) as well as growth of saplings to the 'fire-escape' zone (Bond, Midgley & Woodward 2003).

To our knowledge, only a few empirical studies have addressed the impacts of CO₂ in combination with temperature and precipitation changes on germination and establishment in general (Classen *et al.* 2010) or for relevant encroaching savanna species in particular (but see Polley *et al.* 2002). Supporting our finding that soil moisture plays a key role, Classen *et al.* (2010) found in their experimental study that tree germination and establishment are mostly determined by soil moisture when temperature and CO₂ were increased concurrently. None of the tree species studied showed an increased germination or establishment rate as a result of elevated CO₂ under dry and warm conditions.

Implications for rangeland management

This study shows that the effects of climate change on semi-arid rangelands are highly dependent on the specific scenario. On the one hand, scenarios of increased size of precipitation pulses or increased MAP reveal a stable or even increased carrying capacity of the system. On the other hand, increased interannual variation in precipitation or a decrease in MAP reduces carrying capacities considerably.

Despite this uncertainty, our study reveals that the risk of shrub encroachment will be reduced irrespective of changes in

precipitation pattern because of increased mean temperatures. This has four important implications for rangeland managers and policymakers:

First, a possible loss of woody vegetation in degraded rangelands, especially when this loss is extreme, will pose a new problem to rangeland managers. In particular, at the end of the annual dry season when grass biomass in overutilized areas is depleted, woody plant species contribute significantly to livestock diet (Tainton 1999; Katjiua & Ward 2007). Increased costs for supplemental feeding or the necessity to reduce livestock numbers would be the consequence.

Second, experiences of decision makers derived under present climatic conditions can be misleading for future management (see also Popp *et al.* 2009). If, under future conditions, rangeland managers considered the absence of encroaching bush as a sign of high carrying capacities or well-adapted grazing intensity, they would be at risk of drastically overestimating the carrying capacities of their lands. Therefore, we suggest that sustainable rangeland management in the light of climate change should be determined by available grass biomass and not by woody vegetation cover.

Third, our findings have major implications for medium- and long-term restoration of degraded savanna systems. Declined establishment of woody plants combined with natural senescence of adult plants will lead to a decrease in shrubs in the long run. Thus, elaborate and expensive bush control measures become redundant. The reduced competition from woody species in turn could increase the success of alternative restoration measures such as the (re-)introduction of desired grass species or other investments to improve rangeland quality from both an ecological and an economic perspective.

Finally, savannas are increasingly recognized for their significant contribution to the global carbon cycle (Lehman 2010). An altered risk of degradation and changes in degradation pattern, which both change overall standing biomass, could have major implications in terms of carbon sequestration and the long-term feedback between climate and vegetation (Field *et al.* 2007). Altered carbon sequestration should be considered in the national and international planning of, for example, climate change mitigation and carbon storage projects.

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References

Ainsworth, E.A. & Long, S.P. (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist*, **165**, 351–371.

Blaum, N., Seymour, C., Rossmannith, E., Schwager, M. & Jeltsch, F. (2009) Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. *Biodiversity and Conservation*, **18**, 1187–1199.

Bond, W.J., Midgley, G.F. & Woodward, F.I. (2003) The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Global Change Biology*, **9**, 973–982.

Buitenwerf, R., Swemmer, A.M. & Peel, M.J.S. (2011) Long-term dynamics of herbaceous vegetation structure and composition in two African savanna reserves. *Journal of Applied Ecology*, **48**, 238–246.

Classen, A.T., Norby, R.J., Company, C.E., Sides, K.E. & Weltzin, J.F. (2010) Climate change alters seedling emergence and establishment in an old-field ecosystem. *PLoS ONE*, **5**, e13476, doi:10.1371/journal.pone.0013476.

Drake, B.G., González-Meler, M.A. & Long, S.P. (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.

Engelbrecht, F.A., McGregor, J.L. & Engelbrecht, C.J. (2009) Dynamics of the conforal-cubic atmospheric model projected climate-change signal over southern Africa. *International Journal of Climatology*, **29**, 1013–1033.

Fensham, R.J., Fairfax, R.J. & Archer, S.R. (2005) Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology*, **93**, 596–606.

Field, C.B., Lobell, D.B., Peters, H.A. & Chiariello, N.R. (2007) Feedbacks of terrestrial ecosystems to climate change. *Annual Review of Environment and Resources*, **32**, 1–29.

Fynn, R.W.S. & O'Connor, T.G. (2000) Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology*, **37**, 491–507.

Gillson, L. & Hoffman, M.T. (2007) Rangeland ecology in a changing world. *Science*, **315**, 53–54.

Graz, F.P. (2008) The woody weed encroachment puzzle: gathering pieces. *Ecology*, **1**, 340–348.

Hiernaux, P., Diarra, L., Trichon, V., Mougin, E., Soumaguel, N. & Baup, F. (2009) Woody plant population dynamics in response to climate changes from 1984 to 2006 in Sahel (Gourma, Mali). *Journal of Hydrology*, **375**, 103–113.

IPCC (2007) Climate change 2007: the physical science basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor & H.L. Miller), pp. 996. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jeltsch, F., Weber, G.E. & Grimm, V. (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, **161**, 171.

Jeltsch, F., Milton, S.J., Dean, W.R.J. & van Rooyen, N. (1997) Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science*, **8**, 177–188.

Joubert, D.F., Rothauge, A. & Smit, G.N. (2008) A conceptual model of vegetation dynamics in the semiarid Highland savanna of Namibia, with particular reference to bush thickening by *Acacia mellifera*. *Journal of Arid Environments*, **72**, 2201–2210.

Katjiua, M. & Ward, D. (2007) Pastoralists' perceptions and realities of vegetation change and browse consumption in the northern Kalahari, Namibia. *Journal of Arid Environments*, **69**, 716–730.

Kgope, B.S., Bond, W.J. & Midgley, G.F. (2010) Growth responses of African savanna trees implicate atmospheric [CO₂] as a driver of past and current changes in savanna tree cover. *Austral Ecology*, **35**, 451–463.

Kraaij, T. & Ward, D. (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, **186**, 235–246.

Lehman, C.E.R. (2010) Savannas need protection. *Science*, **327**, 642.

Meissner, H.H. (1982) Theory and application of a method to calculate forage intake of wild southern African ungulates for purposes of estimating carrying capacity. *South African Journal of Wildlife Research*, **12**, 41–47.

Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, T. (2002) *Atlas of Namibia*, 1st edn. David Philip Publishers, Cape Town.

Meyer, K.M., Wiegand, K. & Ward, D. (2009) Patch dynamics integrate mechanisms for savanna tree-grass coexistence. *Basic and Applied Ecology*, **10**, 491–499.

Miller, M.F. (1995) Acacia seed survival, seed-germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. *African Journal of Ecology*, **33**, 194–210.

Morgan, J.A., Pataki, D.E., Korner, C., Clark, H., Del Grosso, S.J., Grunzweig, J.M., Knapp, A.K., Mosier, A.R., Newton, P.C.D., Niklaus, P.A., Nippert, J.B., Nowak, R.S., Parton, W.J., Polley, H.W. & Shaw, M.R. (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*, **140**, 11–25.

Polley, H.W. (1997) Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management*, **50**, 562–577.

- Polley, H.W., Tischler, C.R., Johnson, H.B. & Derner, J.D. (2002) Growth rate and survivorship of drought: CO₂ effects on the presumed tradeoff in seedlings of five woody legumes. *Tree Physiology*, **22**, 383–391.
- Popp, A., Domptail, F., Blaum, N. & Jeltsch, F. (2009) Landuse experience does qualify for adaptation to climate change. *Ecological Modelling*, **220**, 694–702.
- Reynolds, J.F., Kemp, P.R., Ogle, K. & Fernandez, R.J. (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, **141**, 194–210.
- Reynolds, J.F., Stafford Smith, D.M., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernandez, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M. & Walker, B. (2007) Global desertification: building a science for dryland development. *Science*, **316**, 847–851.
- Rothauge, A. (2006) *The Effect of Frame Size and Stocking Rate on Diet Selection of Cattle and Range Condition in the Camelthorn Savanna of East-central Namibia*. PhD Thesis, University of Namibia, Windhoek.
- Sankaran, M., Tatnam, J. & Hanan, N.P. (2004) Tree-grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480–490.
- Scheiter, S. & Higgins, S.I. (2009) Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Global Change Biology*, **15**, 2224–2246.
- Schwinning, S. & Sala, O.E. (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia*, **141**, 211–220.
- Scott, R.L., Huxman, T.E., Cable, W.L. & Emmerich, W.E. (2006) Partitioning of evapotranspiration and its relation to carbon dioxide exchange in a Chihuahuan Desert shrubland. *Hydrological Processes*, **20**, 3227–3243.
- Skarpe, C. (1990) Shrub layer dynamics under different herbivore densities in an arid Savanna, Botswana. *Journal of Applied Ecology*, **27**, 873–885.
- Tadross, M., Jack, C. & Hewitson, B. (2005) On RCM-based projections of change in southern African summer climate. *Geophysical Research Letters*, **32**, L23713, DOI: 10.1029/2005GL024460.
- Tainton, N.M. (1999) *Veld Management in South Africa*, 1st edn. University of Natal Press, Pietermaritzburg.
- Tews, J., Schurr, F. & Jeltsch, F. (2004) Seed dispersal by cattle may cause shrub encroachment of *Grewia* lava on southern Kalahari rangelands. *Applied Vegetation Science*, **7**, 89–102.
- Tietjen, B. & Jeltsch, F. (2007) Semi-arid grazing systems and climate change: a survey of present modelling potential and future needs. *Journal of Applied Ecology*, **44**, 425–434.
- Tietjen, B., Zehe, E. & Jeltsch, F. (2009) Simulating plant water availability in dry lands under climate change: a generic model of two soil layers. *Water Resources Research*, **45**, W01418, doi:10.1029/2007WR006589.
- Tietjen, B., Jeltsch, F., Zehe, E., Classen, N., Groengroeft, A., Schiffers, K. & Oldeland, J. (2010) Effects of climate change on the coupled dynamics of water and vegetation in drylands. *Ecohydrology*, **3**, 226–237.
- UNCCD (1994) United Nations Convention to Combat Desertification, Elaboration of an International Convention to Combat Desertification in Countries Experiencing Serious Drought and/or Desertification, Particularly in Africa (U.N. Doc. A/AC.241/27, 33 I.L.M. 1328, United Nations).
- Vetter, S. (2005) Rangelands at equilibrium and non-equilibrium: recent developments in the debate. *Journal of Arid Environments*, **62**, 321–341.
- Ward, D. & Esler, K.J. (2011) What are the effects of substrate and grass removal on recruitment of *Acacia mellifera* seedlings in a semi-arid environment? *Plant Ecology*, **212**, 245–250.
- Weber, G.E. & Jeltsch, F. (2000) Long-term impacts of livestock herbivory on herbaceous and woody vegetation in semiarid savannas. *Basic and Applied Ecology*, **1**, 13–23.
- Westoby, M., Walker, B. & Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 266–274.
- Wiegand, K., Ward, D. & Saltz, D. (2005) Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. *Journal of Vegetation Science*, **16**, 311–320.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Parameters of vegetation model.

Table S2. Parameters of hydrological model.

Appendix S1. Model rules.

Appendix S2. Model validation and sensitivity analyses.

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