Effects of climate change on the coupled dynamics of water and vegetation in drylands

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ABSTRACT

Drylands worldwide are exposed to a highly variable environment and face a high risk of degradation. The effects of global climate change such as altered precipitation patterns and increased temperature leading to reduced water availability will likely increase this risk. At the same time, an elevated atmospheric CO_2 level could mitigate the effects of reduced water availability by increasing the water use efficiency of plants. To prevent degradation of drylands, it is essential to understand the underlying processes that affect water availability and vegetation cover. Since water and vegetation are strongly interdependent in water-limited ecosystems, changes can lead to highly non-linear effects. We assess these effects by developing an ecohydrological model of soil moisture and vegetation cover. The water component of the model simulates the daily dynamics of surface water and water contents in two soil layers. Vegetation is represented by two functional types: shrubs and grasses. These compete for soil water and strongly influence hydrological processes. We apply the model to a Namibian thornbush savanna and evaluate the separate and combined effects of decreased annual precipitation, increased temperature, more variable precipitation and elevated atmospheric CO_2 on soil moisture and on vegetation cover. The results show that two main factors control the response of plant types towards climate change, namely a change in water availability and a change in water allocation to a specific plant type. Especially, reduced competitiveness of grasses can lead to a higher risk of shrub encroachment in these systems. Copyright © 2009 John Wiley & Sons, Ltd.

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KEY WORDS   climate change; CO_2; drylands; ecohydrology; model; precipitation; savanna; shrub encroachment; temperature

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INTRODUCTION

Drylands form nearly 30% of the global land surface (Stafford Smith, 1996; Sivakumar *et al*., 2005) and are characterized by a tight coupling of water availability and vegetation dynamics (Noy-Meir, 1973). Because of the extremely variable climatic conditions, the risk of deterioration is high. For example, under unfavourable conditions, often going along with high grazing pressure, bare patches of soil can arise (Rietkerk and van de Koppel, 1997; Kefi *et al*., 2007) or the fragile equilibrium between woody and herbaceous vegetation can shift towards a shrub-dominated state (Roques *et al*., 2001). Once a degraded state is reached, regeneration is hardly feasible and a reduction in biodiversity or in productivity for livestock farming is likely.

Climate change will probably increase this risk. Worldwide, drylands are threatened by decreasing mean annual precipitation (MAP) (Dore, 2005). Generally, the frequency of precipitation events decreases; however, the number of extreme events increases. (Easterling *et al*.,

2000). Moreover, higher temperatures are likely to intensify water stress through increased evapotranspiration (Hughes, 2003). At the same time, increased atmospheric CO_2 could mitigate these effects directly by higher photosynthetic rates of plants, and indirectly by enhancing the water use efficiency (Bazzaz 1990; Drake *et al*., 1997).

Clearly, different plant types are not affected equally by these changes. For example, maximum woody cover has been found to increase linearly with a MAP below 650 mm in arid and semi-arid savannas (Sankaran *et al*., 2005), accompanied by a reduction in grass cover. In addition to mean annual values, the timing, intensity and duration of precipitation as well as soil properties can strongly determine water availability. Soil moisture recharge in the subsoil occurs only if precipitation events are clustered or very intense. Here, water is better protected against evaporation than in the topsoil layer, where moisture fluctuations can be very rapid (Noy-Meir 1973; Schwinning *et al*., 2001). Thus, depending on the potential rooting depth of plants, their actual access to water can be quite different. Moreover, the response time and intensity of plants to increased soil moisture can vary across plant species (Fravolini *et al*., 2005) and between their life history stages (Beatley, 1974).

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Also, the effects of elevated atmospheric CO_2 vary strongly between plant types. In a meta-analysis of free-air CO_2 enrichment experiments, Ainsworth and Long (2005) reported the highest increase of dry matter production for woody vegetation followed by legumes and C_3 grasses. No significant increase was found for species following the C_4 photosynthetic pathway. This is caused by the strong limiting effect of CO_2 on C_3 plants under ambient CO_2 concentrations in contrast to C_4 plants (Morgan *et al.*, 2004). Bond *et al.*, (2003) suggested that, especially, growth rate of juvenile C_3 trees with a high carbon demand could be sensitive to an increased CO_2 level, which could alter the tree grass balance. Other studies also report a response of C_4 plants to elevated atmospheric CO_2 (e.g. Poorter, 1993; Anderson *et al.*, 2001), since the indirect effect of increased water use efficiency of plants holds also for C_4 species (Körner, 2006). In summary, elevated CO_2 generally exerts positive effects on the growth of various plant types. However, the relative magnitude of this effect varies among plant types, so that species composition can shift considerably.

These potential changes in vegetation cover and species composition will in turn strongly feedback on the water balance. Plants may facilitate their own growth by promoting infiltration, by decreasing run-off water as a result of higher surface roughness, and by preventing nutrient losses due to erosion of the top soil (van de Koppel *et al.*, 2000). Additionally, shading by plants leads to reduced evaporation and thereby improves the storage efficiency of shallow soils. The importance of these positive feedbacks increases with increasing abiotic stress (Bertness *et al.*, 1994; Callaway *et al.*, 1997). On the other hand, water losses due to transpiration increase with vegetation density, leading to faster water losses, especially in the deeper soil, and thus to increased competition among individual plants.

This interplay of temporally limited water availability and facilitation and competition among plants has been found to be particularly important in savannas, being defined as landscapes with a more or less continuous grass layer and scattered woody plants (Scholes and Archer 1997). Savannas can be found under a broad range of climatic conditions, with annual precipitation ranging from less than 100 mm to more than 1500 mm (Jeltsch *et al.*, 2000) and are widely used for the production of livestock. To predict the dynamics of the complex interactions between water and vegetation, several models have been developed (Klausmeier, 1999), especially for assessing the conditions for livestock grazing (Jeltsch *et al.*, 1996; van Langevelde *et al.*, 2003; Higgins *et al.*, 2007). However, these models usually aggregate intra-annual water fluctuations to monthly or yearly sums and do therefore not capture the impacts of single precipitation events. Under present climate conditions this does not necessarily have to be problematic, and long-term vegetation dynamics can often be simulated adequately. However, if the patterns of precipitation pulses or other driving factors are temporally highly variable (Baudena *et al.*, 2007) or are altered in the course of climate change,

assumptions being valid for present conditions are not necessarily transferable anymore. In this case, integrated approaches are needed that allow for evaluating the non-linear effects of altered climatic conditions on the coupled water and vegetation dynamics. These approaches are widely missing as a review of more than 40 models published between 1995 and 2005 showed (Tietjen *et al.*, 2007).

In this study, we therefore propose a coupled water-vegetation model for drylands (*EcoHyD* — **Ec**o**Hy**drology in **D**rylands) to explore the effects of climate change on soil moisture and vegetation cover. This combined ecohydrological approach accounts for the intensity and duration of single precipitation events and the resulting dynamics of two plant life forms, namely grasses and shrubs. Additionally, the model allows for evaluating separate and combined effects of increased temperature and atmospheric CO_2 on water and vegetation. We applied this model to a Namibian thorn bush savanna and analysed the following questions: (1) what are the separate effects of changes in precipitation, temperature, and CO_2 on soil moisture and vegetation cover, and (2) what are the combined effects of these changes, i.e. what do we have to expect under future climate change.

MODEL DESCRIPTION (*ECOHYD*)

We linked the grid-based model *HydroVeg* of daily moisture dynamics in two soil layers (Tietjen *et al.*, 2009) with a vegetation model (Figure 1). The size of one grid cell is 5 m by 5 m and the total extent covers 10,000 cells corresponding to an area of 25 ha. Each cell is characterized by a topographic height, and we chose open boundary conditions to allow for water losses by run-off.

Vegetation is divided into two plant life form types, namely shrubs and grasses (perennial herbaceous vegetation). For each type, vegetation cover c_{veg} [% per cell] and its change are determined by the processes growth (gr_{veg}), mortality (m_{veg}), and dispersal and establishment (d_{veg}), with the subscription *veg* referring to shrubs (*s*) and grass (*g*):

$$\frac{dc_{veg}}{dt} = gr_{veg} - m_{veg} + d_{veg} \qquad 1$$

Vegetation growth is calculated biweekly during the wet season, which we determine for each year as the time between the first effective rain event of the season with precipitation $P \geq 5$ mm and the last rain event plus 14 days. Mortality due to water stress and dispersal is evaluated at the end of a fixed growing season as a result of the mean seasonal soil moisture. No change in vegetation is assumed during the dry season.

Plant growth

Vegetation growth can be split into the sum of growth induced by water in the upper and the lower soil layers ($gr_{veg,L1}$ and $gr_{veg,L2}$, respectively) and is assumed
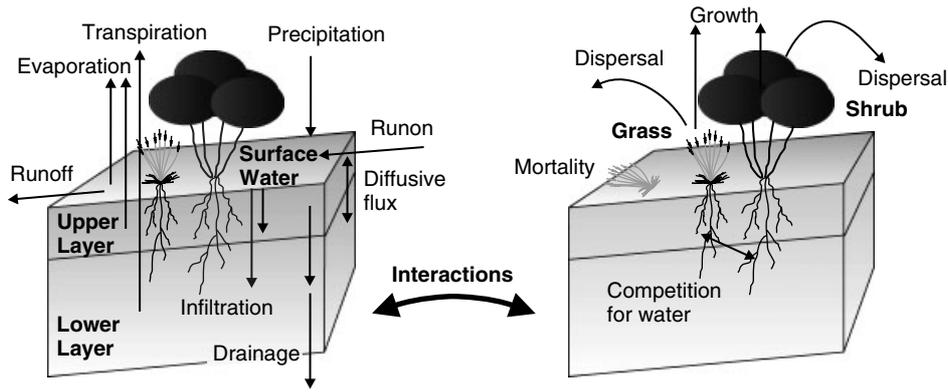
Figure 1. Model overview. Main processes and system components of the hydrological model and the vegetation model in one grid cell.

to follow logistic behaviour with growth rate r_{veg} [mm^{-1} yr^{-1}]. Growth is reduced, if water availability for one vegetation type $avW_{veg,Lx}$ [mm] in layer x is limited or competition is high, which leads to a reduced relative water uptake per unit cover $U_{veg,Lx}$ [dimensionless]:

$$gr_{veg,Lx} = \min(U_{veg,Lx} \cdot avW_{veg,Lx}, 1) \cdot r_{veg} \cdot$$
$$c_{veg} \cdot \left(1 - \frac{c_{veg}}{1 - (c_{\neg veg} - lap)} \right) [\text{yr}^{-1}] \qquad 2$$

The maximum cover in the logistic growth term depends on its own cover [%], on the cover of the respective other plant type $c_{\neg veg}$ [%], and on the potential overlapping lap [dimensionless] of both types. Overlapping occurs if one plant type grows directly under the other one. Soil moisture availability is calculated depending on the amount of water above the plant specific wilting point $W_{wp,veg}$ [vol%]:

is assumed fixed independent of the respective cover or adaptive mechanisms.

Plant mortality

Calculated mortality occurs at the end of the growing season as a result of unfavourable soil moisture conditions during the whole season. This allows for evaluating long-term effects of water stress. Analogous to growth, we calculate mean seasonal water availability to sustain important life functions $sustW_{Lx}$ [mm] in each layer x:

$$sustW_{Lx} = (W_{Lx,\text{mean}} - W_{wp,veg}) \cdot depth_{Lx} [\text{mm}] \qquad 5$$

with $W_{Lx,\text{mean}}$ [vol%] the mean soil moisture in layer x during the growing season. Mortality of each plant type

$$avW_{veg,Lx} = \begin{cases} 0 & W_{Lx} \le W_{wp,veg} \\ (W_{Lx} - W_{wp,veg}) \cdot depth_{Lx} & \text{else} \end{cases} [\text{mm}] \qquad 3$$

with W_{Lx} [vol%] the mean water content in layer x during the previous 14 days and $depth_{Lx}$ [mm] the depth of the respective layer. That is, water availability for plants is zero below the plant-type specific wilting point and afterwards increases linearly. Extending the approach by Walker *et al*., (1981) and van Langevelde *et al*., (2003), which was originally developed for a single soil compartment, the fraction of the available water that can be taken up per unit cover can be calculated as

$$U_{veg,Lx} = \frac{\theta_{veg} \cdot root_{veg,Lx}}{\theta_g \cdot root_{g,Lx} \cdot c_g + \theta_s \cdot root_{s,Lx} \cdot c_s}$$
$$[\text{dimensionless}] \qquad 4$$

where the relative uptake depends on competition between grasses and shrubs, which is described by their current cover, the potential uptake rate per cover θ_{veg} [mm yr^{-1}], and the fraction of roots $root_{veg,Lx}$ of the respective vegetation type in the layer x. As a simplification, the vertical root distribution of the two vegetation types

in each layer $m_{veg,Lx}$ is then calculated as a function dependent on water availability, the plant-type specific mortality rate mr_{veg} [mm^{-1} yr^{-1}], the proportional uptake $U_{veg,Lx}$ of this water, and current vegetation cover c_{veg}. Additionally, the relative dependence of a vegetation type on water in the respective layer is accounted for by the root distribution:

$$m_{veg,Lx} = mr_{veg} \cdot c_{veg} \left[(1 - \min(U_{veg,Lx} \cdot sustW_{Lx}, 1)) \cdot \frac{root_{veg,Lx}}{\sum\limits_{i} root_{veg,Li}} \right] [\text{yr}^{-1}] \qquad 6$$

Total mortality is then given by the sum of mortality caused by unfavourable conditions in each layer.

Dispersal and establishment

Grass seeds are normally not dispersal limited in such a small area (Jeltsch *et al.*, 1997), and we therefore assume them to spread spatially homogeneously in space. The amount of dispersed seeds depends on the mean grass cover within the whole grid area. In contrast, shrub dispersal is strongly limited (Wiegand *et al.*, 1995; Jeltsch *et al.*, 1998; Witkowski *et al.*, 2000). Here, we chose an exponential decrease of dispersed seed number with Euclidean distance (*dist*) from the source cell (*sc*). If the seasonal mean soil moisture $W_{L1,mean}$ of the upper layer of the target cell is above the plant-type specific wilting point, seedlings can establish depending on the current vegetation cover. Here, an important demographic bottleneck can occur, if recruitment is limited by water availability (see a debate on demographic bottlenecks in savannas in Sankaran *et al.*, 2004). Actual establishment of grasses and shrubs (d_g and d_s) in one cell due to dispersal originated from source cell *sc* is calculated as:

$$d_g = \begin{cases} 0 & \text{if } W_{L1,mean} < W_{wp,g} \; [\text{yr}^{-1}] \\ c_{g,mean} \cdot e_g \cdot \max(1 - c_g - c_s, 0) & \text{else} \end{cases}$$

$$d_s = \begin{cases} 0 & \text{if } dist \geq dist_{max,s} \; or \; W_{L1,mean} < W_{wp,s} \; [\text{yr}^{-1}] \\ c_{s,sc} \cdot e_s \cdot d_{0,s} \cdot e^{-cd \cdot dist} \cdot \max(1 - c_g - c_s, 0) & else \end{cases} \qquad 7$$

The constant e_{veg} [dimensionless] describes the rate of successful establishment and the constants $d_{0,s}$ and *cd* [dimensionless] determine the decline of the exponential function with distance. The exponential function is cut off at a maximal dispersal distance $dist_{max,s}$ [m].

Soil moisture dynamics

Soil moisture is determined by several processes, which are closely linked to vegetation cover. Surface water (W_{SF}) is increased by precipitation (*PI*) and can infiltrate into the upper layer (W_{L1}) or via macropores also into the lower soil layer (W_{L2}). Infiltration into the upper and lower layer (F_{L1} and F_{L2}) depends on surface water height, the water content in the destination layer, and grass and shrub cover. If the topsoil hydraulic conductivity is low or precipitation events are extreme, run-off can occur and water is redistributed from higher to lower cells (Q_{out} generated run-off, Q_{in} received run-off from surrounding cells). Surface water can evaporate (ET_{SF}), with shading by vegetation cover leading to reduced evaporation.

$$\frac{dW_{SF}}{dt} = PI - F_{L1}(W_{SF}, W_{L1}, c_g, c_s) - F_{L2}(W_{SF}, c_s)$$
$$- ET_{SF}(W_{SF}, c_g, c_s) - Q_{out}(W_{SF}, c_g, c_s)$$
$$+ Q_{in} [\text{mm h}^{-1}] \qquad\qquad 8$$

Excess water in the soil can drain to lower layers ($F_{drainL1}, F_{drainL2}$), and it is considered as lost in case of drainage from the lower layer. Additionally, the water content of the two layers is balanced slowly by diffusive fluxes between the layers (F_{L1L2}). Water from both layers is lost by evapotranspiration (ET_{L1}, ET_{L2}), which depends on vegetation cover, radiation, temperature and the slope and aspect of the cell.

$$\frac{dW_{L1}}{dt} = F_{L1}(W_{SF}, W_{L1}, c_g, c_s) - F_{drainL1}(W_{L1})$$
$$- F_{L1L2}(W_{L1}, W_{L2})$$
$$- ET_{L1}(W_{L1}, c_g, c_s) [\text{mm h}^{-1}] \qquad 9$$

$$\frac{dW_{L2}}{dt} = F_{L2}(W_{SF}, c_s) + F_{drainL1}(W_{L1})$$
$$- F_{drainL2}(W_{L2}) + F_{L1L2}(W_{L1}, W_{L2})$$
$$- ET_{L2}(W_{L2}, c_s) [\text{mm h}^{-1}] \qquad 10$$

A detailed description of the soil moisture model and its linkage to vegetation cover can be found in Tietjen *et al.*, (2009).

SITE DESCRIPTION AND PARAMETERIZATION

We applied the model to a Namibian thorn bush savanna that is situated approximately 45 km north of Okahandja in the Otjozontjupa region (latitude: 21·6 °S, longitude: 16·9 °E). Precipitation falls during the summer months (September to April) and is highly variable between years with a MAP of approximately 360 mm with a standard deviation of 130 mm. The annual mean temperature is about 20 °C, with monthly means ranging from 13 °C in July to 27 °C in January. We generated long-term climate data for 100 years with the rainfall generator ReGen (Köchy, 2006). The generated rain (model parameters of ReGen: MAP: 360 mm; ΔDMR an optional factor influencing the amplitude of a single rain event: 0·2) matches main characteristics of rain data from the study region: an analysis of variance (anova) showed no significant differences between measured precipitation data of 20 years and generated precipitation in monthly precipitation sums ($F_{1,1442} = 0.0802$, $p = 0.6752$) and in the coefficient of variation of daily precipitation within one month ($F_{1,769} = 1.9577$, $p = 0.1622$). Daily precipitation data was interpolated to hourly values as described in Tietjen *et al.* (2009). Daily and hourly temperature values (T_{day}, T_{hour}) were fitted by a cosine function to seven years of measured data from 2001 to 2007:

$$T_{day} = T_{year} + T_{diff,year} \cdot \cos\left((day + 190)\tfrac{2\pi}{365}\right)$$
$$T_{hour} = T_{day} + T_{diff,day} \cdot \cos\left((hour - 3)\tfrac{2\pi}{24}\right)$$

Table I. Standard parameters of the soil water model. For full descriptions see Tietjen *et al.* (2009).

Name	Description	Value	Unit	Source
Infiltration				
K_s	Saturated hydraulic conductivity	17·6	mm/h	Measured (N. Classen, unpublished)
sf	Effective suction at wetting front	110·1	mm	Rawls *et al.* (1992)
$F_{L2,bare}$	Bare soil infiltration rate	0	—	Deep infiltration is not relevant at these sites
$F_{L2,frac}$	Infiltration rate	0	—	
$F_{L2,max}$	Maximal total infiltration	0	mm/h	
Slow diffusion				
d	Water balancing constant between layers	0·05	—	Estimated according to Bai *et al.* (2007)
Evapotranspiration				
TE	Change in transpiration efficiency		—	Set in the CO_2 scenarios according to Ainsworth and Long (2005)
Specific soil water contents				
wsc	Water content of beginning stomatal closure (pF = 4·2)[a]	7·9	vol%	Measured (N. Classen, unpublished)
fc	Field capacity (pF = 1·8)[a]	22·6	vol%	Measured (N. Classen, unpublished)
rw	Residual water content during the dry season	6·0	vol%	Measured (N. Classen, unpublished)
Soil depths				
$depth_{L1}$	Depth of the upper soil layer	200	mm	Measured (N. Classen, unpublished)
$depth_{L2}$	Depth of the lower soil layer	600	mm	Measured (N. Classen, unpublished)

[a] pF value: soil water content that corresponds to a logarithmic soil water potential of 4·2 and 1·8, respectively.

with mean yearly temperature $T_{year} = 20.0\,°C$, mean yearly fluctuations in temperature $T_{diff,year} = 7.5\,°C$, mean daily fluctuations $T_{diff,day} = 5.0\,°C$, and *day* starting on 1 July.

The topography of the area is very flat (mean slope: 0·9%) with a mean height of 1500 m above sea level. A digital elevation model was only available in a resolution of 100 m by 100 m, which we interpolated linearly to a resolution of 5 m by 5 m. The dominant soil texture is a sandy loam (sum of silt and clay in 0–10 cm depth: 35%, 10–30 cm: 45%, 30–60 cm: 48%) and is partly underlain by calcrete. In our analysis we assumed homogeneous soil conditions in the simulated area of 25 ha. The corresponding soil parameters are given in Table I, a full description of these parameters can be found in Tietjen *et al.* (2009).

The potential natural vegetation is an open thorn bush savanna with Acacia species as dominant woody components (e.g. *Acacia mellifera, A. reficiens*) and herbaceous species such as *Stipagrostis uniplumis, Aristida* sp. and *Eragrostis* sp. Fires occur only occasionally. Since the 1950s, extensive cattle and game farming have led to shrub encroachment in some spots with dense thickets of *A. mellifera*. Since the end of the last century, livestock density was kept lower and the grass cover improved. Standard parameters for the vegetation model are given in Table II.

SIMULATION EXPERIMENTS

Baseline scenario and sensitivity analysis

The baseline scenario is simulated in *EcoHyD* with standard model parameters given in Tables I and II. Initial vegetation cover is homogeneously set to 40% for grass and 15% for shrubs, corresponding to values that have been found in the field under moderate grazing conditions. We first compared simulation results of grass cover with values found in the field from 2001 to 2005 to gain confidence in model results. Afterwards, we performed five simulations of 100 years to demonstrate an arising steady state of grass and shrub cover. To assess the sensitivity of model results, we systematically modified all vegetation parameters by ±10% and ±20% (exceptions: (1) $W_{wp,g}$, $W_{wp,s}$: here we varied the distance to the residual water content by ±10% and ±20%, and (2) first and last day of the growing season (gStart, gEnd): here we shifted the value by ±10 days and ±20 days). Afterwards, we evaluated the effect of these changes on mean soil moisture during the growing season in both layers and mean vegetation cover during the whole year. For this, we performed simulations of 100 years, whereof the last 20 years where evaluated.

Climate change scenarios

We evaluated the separate and combined effects of four possible climatic change results: (1) decreased mean precipitation, (2) increased temperature, (3) an increase in extreme events with a fixed mean precipitation and (4) increased atmospheric CO_2 level. For scenario (1) we used the model ReGen (Köchy, 2006) to generate new precipitation time series with mean precipitation amounts of 300, 315, 330, 345, and 360 mm, which lie in the predicted range for the A1B scenario for the years 2080 to 2099 (IPCC, 2007). To change temperature, a main determinant of evapotranspiration, in scenario (2) we followed the IPCC also and increased the mean annual temperature by 0·75, 1·5, 2·25, and 3·0 C. A more variable precipitation as described by Easterling *et al.* (2000) was generated in scenario (3) by shifting the total precipitation amount of events falling into the

Table II. Standard parameters and their values used in the vegetation model.

Name	Description	Value	Unit	Source
Growth				
$W_{wp,g}$	Grass specific wilting point	6·4	vol%	Mean value of Sala *et al.* (1989) and Neilson (1995)
$W_{wp,s}$	Shrub specific wilting point	6·3	vol%	Mean value of Sala *et al.* (1989) and Neilson (1995)
θ_g	Potential uptake rate per unit grass cover	$7·2 \cdot 10^6$	mm yr^{-1}	$\theta_g = \theta_{BM,g} \cdot \text{conv}BMToC_g$
	$\theta_{BM,g} = 0.9$ mm/(yr*g) relative uptake rate per gram grass biomass (van Langevelde *et al.*, 2003) conv$BMToC_g$ = 8·0E +06 g conversion: grass biomass to relative cover (J. Oldeland, unpublished)			
θ_s	Potential uptake rate per unit shrub cover	$2·5 \cdot 10^7$	mm yr^{-1}	$\theta_s = \theta_{BM,s} \cdot \text{conv}BMToC_s$
	$\theta_{BM,s} = 0.5$ mm/(yr*g) relative uptake rate per gram shrub biomass (van Langevelde *et al.*, 2003) conv$BMToC_s$ = 5·0E +07 g conversion: shrub biomass to relative cover (J. Oldeland, unpublished)			
$\text{root}_{g,L1}$	Fraction of grass roots in the upper layer	0·63	—	$\text{root}_{g,L1} = 1 - \beta_g^d$ $\beta_g = 0·952$, d = 20 cm (Jackson *et al.*, 1996)
$\text{root}_{g,L2}$	Fraction of grass roots in the lower layer	0·37	—	$1 - \text{root}_{g,L1}$
$\text{root}_{s,L1}$	Fraction of shrub roots in the upper layer	0·36	—	$\text{root}_{s,L1} = 1 - \beta_s^d$ $\beta_s = 0·978$, d = 20 cm (Jackson *et al.*, 1996)
$\text{root}_{s,L2}$	Fraction of shrub roots in the lower layer	0·64	—	$1 - \text{root}_{s,L1}$
r_g	Potential growth rate of grass	0·8	mm^{-1} yr^{-1}	Calibrated to gain long-term values with a mean grass cover of 40–80% and a mean shrub cover of 15–25% observations (J. Oldeland, unpublished)
r_s	Potential growth rate of shrubs	0·2	mm^{-1} yr^{-1}	
lap	maximal extent to which grass and shrubs can overlap	20	%	
Mortality				
W_{res}	Residual soil water content	6·0	vol%	Measured data (N. Classen, unpublished)
mr_g	Mortality rate of grass due to water stress	0·9	mm^{-1} yr^{-1}	van Langevelde *et al.*, (2003)
mr_s	Mortality rate of shrubs due to water stress	0·4	mm^{-1} yr^{-1}	van Langevelde *et al.* (2003)
Dispersal				
e_g	Rate of successful establishment of grasses	0·05	yr^{-1}	Estimated value, low sensitivity
e_s	Rate of successful establishment of shrubs	0·005	yr^{-1}	Estimated value, low sensitivity
$d_{0,s}$	Constant for exponential dispersal decline with distance	0·5	—	Values are chosen in a way that the cumulative dispersal is 75% at dist = 2·5 m (border of a cell) and 99% at dist$_{max}$
cd	Constant for exponential dispersal decline with distance	0·53	—	
$\text{dist}_{max,s}$	Maximal distance of shrub seed dispersal	20	m	short distance dispersal only, e.g. Jeltsch *et al.* (1996)
Other				
gStart	Starting day of the growing season (since July 1)	150	—	long-term soil moisture observations in the model
gEnd	Last day of the growing season (since July 1)	330	—	long-term soil moisture observations in the model

lowest quantile (10, 20, 30 and 40%) to precipitation events falling into the upper 90% quantile, while keeping the MAP fixed. An increased atmospheric CO_2 level in scenario (4) was simulated (i) by increasing the water use efficiency (transpiration efficiency TE) of plants, (ii) by increasing TE and the potential growth rate solely of shrubs, and (iii) by increasing TE and the potential growth rates of both, shrubs and grasses. These three CO_2 scenarios were chosen to cover a broad range of possible effects of increased CO_2 on the coupled water and vegetation dynamics. Literature agrees on the positive effect of CO_2 on the transpiration efficiency; therefore, we included higher TE in all CO_2 scenarios by decreasing transpiration in the hydrological model in the lower layer by 10, 20, 30 and 40% in accordance to mean responses found in free-air CO_2 enrichment experiments (Ainsworth and Long, 2005). The response in growth of plants to elevated CO_2 conditions is difficult to quantify for plant types. Tropical grasslands are typically dominated by grasses with the C_4 photosynthetic pathway (Polley, 1997), which are generally less responsive to elevated CO_2 than plants with the C_3 pathway, since C_4 photosynthesis is often saturated or nearly saturated under ambient concentrations (Morgan *et al.*, 2004). Therefore, in the scenarios with an increased growth rate of vegetation, we distinguished whether this applied also

Table III. Parameters for combined effects of climate change.

Scenario	Precipitation (mm yr^{-1})	Temperature change (°C)	Extreme events: shifted quantile (%)	Growth rate of grass (mm^{-1} yr^{-1})	Growth rate of shrubs (mm^{-1} yr^{-1})	Increase in transpiration efficiency (%)
0	360	0·0	0	0·8	0·2	0
1	345	0·75	10	0·85	0·25	10
2	330	1·5	20	0·9	0·3	20
3	315	2·25	30	0·95	0·35	30
4	300	3·0	40	1	0·4	40
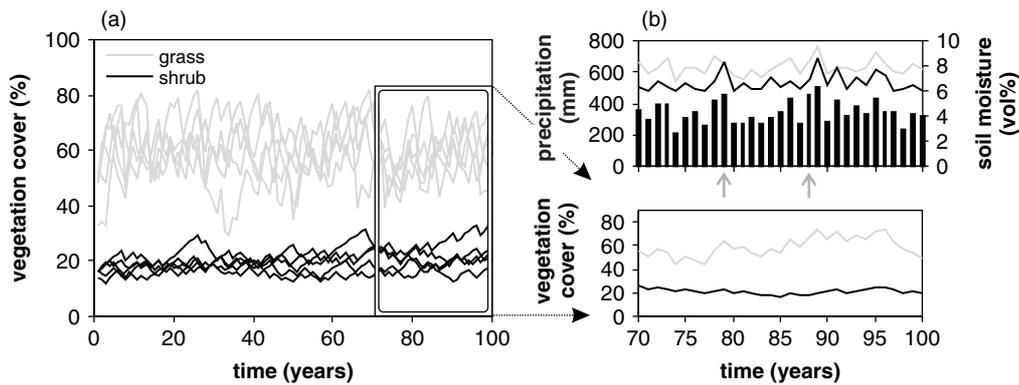
Figure 2. Vegetation cover under present climatic conditions. (a) Five sample 100-year simulations runs with standard parameter set; (b) last 30 years of one simulation with the underlying precipitation (bars) and the corresponding mean soil moisture in the upper layer (grey line) and the lower layer (black line). Grey arrows indicate simulation year 79 and 88, respectively.

for grasses or solely for shrubs. Following Bond *et al.* (2003) we assumed a maximal increase in the growth rate of shrubs by 90% and of grasses by 30% for an increase of atmospheric CO_2 from 360 ppm to 700 ppm and chose growth rates of 0·8, 0·85, 0·9 and 1·0 mm^{-1} yr^{-1} for grasses and 0·2, 0·25, 0·3, 0·35, 0·4 and 0·45 mm^{-1} yr^{-1} for shrubs.

Afterwards, we evaluated the combined effect of these scenarios with the parameter combination given in Table III, to demonstrate a possible future scenario. For increased CO_2 we again simulated the three scenarios introduced above.

To even the effects of stochastic rainfall, all scenarios were repeated five times with the results of different rain simulations by ReGen. We analysed the impacts of these scenarios on mean soil moisture during the growing season and on vegetation cover during the last 20 years of 100 years of simulation.

RESULTS

Baseline scenario and sensitivity analysis

The comparison of simulated data with measured data is given in Appendix A1 (supporting information). Although measured grass cover refers only to the dynamics of 5 years on 12 plots, and simulated grass cover refers to the dynamics of the last 50 years of one 100-year

simulation experiment, the good correspondence between the magnitudes of results improves our confidence with the model.

Independent of climate variations and of the initial vegetation cover, vegetation stabilizes in the last 50 years of the simulation at a dynamic equilibrium cover for grasses and shrubs at about 60% and 20%, respectively (Figure 2a). Since the topography of the simulated site is very flat, and lateral water fluxes by run-off are very low (<1% of precipitation), spatial heterogeneity in water availability and vegetation cover is low and we therefore show only mean results. However, simulations at sites with a more pronounced topography showed that under these conditions water availability depends strongly on flow routing and thus spatially highly heterogeneous (Tietjen *et al.*, 2009). Vegetation cover is characterized by high inter-annual fluctuations of grass cover (standard deviation: 8·8%) depending on the climatic conditions and on lower fluctuations of shrub cover (standard deviation 2·7%). Annual precipitation is highly variable (Figure 2b). But contrary to a common assumption in savanna models, high rainfall does not necessarily lead to high soil moisture: while soil moisture in both layers is well above average in year 79 of the simulation with 459 mm of rain (upper layer: 8·2 vol%, lower layer: 8·3 vol%), soil moisture in the lower layer is rather low under similar rainfall conditions in year 88 (450 mm rain, upper layer: 8·5 vol%, lower layer: 6·9 vol%).

The sensitivity of model results towards uncertainties of the input parameters is given in Appendices A2 and A3. Overall, soil moisture during the growing season and vegetation cover show a very low sensitivity towards vegetation parameters. Soil moisture generally varies within a range of less than 0·1 vol% for a 10% change in parameter value (0·2 vol% for a 20% change), and vegetation cover varies less than 5% for grasses and less than 2% for shrubs (20% change in parameters: maximal 10% for grasses and 5% for shrubs). In contrast to the low sensitivity towards other parameters, soil moisture in the upper layer is sensitive to the starting and ending point of the growing season (*gStart, gEnd*): Generally, a shorter time period of the growing season leads to higher soil moisture content, since rain is even less reliable at the beginning and ending of the growing season. However, this does not reflect in vegetation cover. Especially grass is sensitive to the fraction of grass roots in the upper soil layer, since a lower fraction leads to a reduced competitiveness. Therefore, care should be applied when determining the distribution of grass roots. Generally, a doubling in the change of vegetation parameters from 10% to 20% leads to a doubling of the change in results, i.e. the response to changes seems to be linear.

Climate change

The manifold aspects of climate change lead to quite diverse responses of soil moisture and the corresponding grass and shrub cover. A reduction in the MAP leads to an overall decrease in soil moisture and thus to a lower vegetation cover (Figure 3a). Although mainly the upper soil layer suffers from decreased precipitation, this impacts mostly shrubs: a reduction from 360 mm to

300 mm leads to cover losses of about 10%, while grasses benefit at first from reduced competition with shrubs and decrease only for very high reductions in precipitation. In contrast, an increase in temperature affects grass and shrubs similarly (Figure 3b). Here, soil moisture in the upper layer decreases by up to 1·0 vol% resulting in cover losses of both plant types. More variable and extreme precipitation within 1 year has little effect on soil moisture in the upper layer (Figure 3c). However, the lower soil layer benefits from more extreme events, since water recharge is more efficient due to more intense rain events. The water content in the lower layer increases slightly. This has positive effects on shrub cover, which is increased by 10%.

The combined effects of an elevated atmospheric CO_2 level, i.e. higher transpiration efficiency and increased growth rates, are ambiguous (Figure 3d, solid lines). Overall, soil moisture in the upper layer is unaffected, and moisture in the lower layer is slightly reduced, even though water losses are reduced due to the higher transpiration efficiency. This is caused by the strong increase in shrubs, which extract more water from the lower layer. In contrast, grass cover declines despite its higher growth rate. That is, the altered conditions seem to benefit shrubs, which in turn suppress the growth of grasses. This effect is even intensified in the case of the CO_2 scenario with constant grass growth, i.e. where the photosynthetic rate of grasses is assumed to remain unaffected by an elevated atmospheric CO_2 level. Here, the system shifts towards a shrub-dominated state. If the growth rate of shrubs is also assumed to remain unaffected, the sole effect of increased transpiration has little effects on soil moisture and vegetation cover: only shrub cover increases slightly.
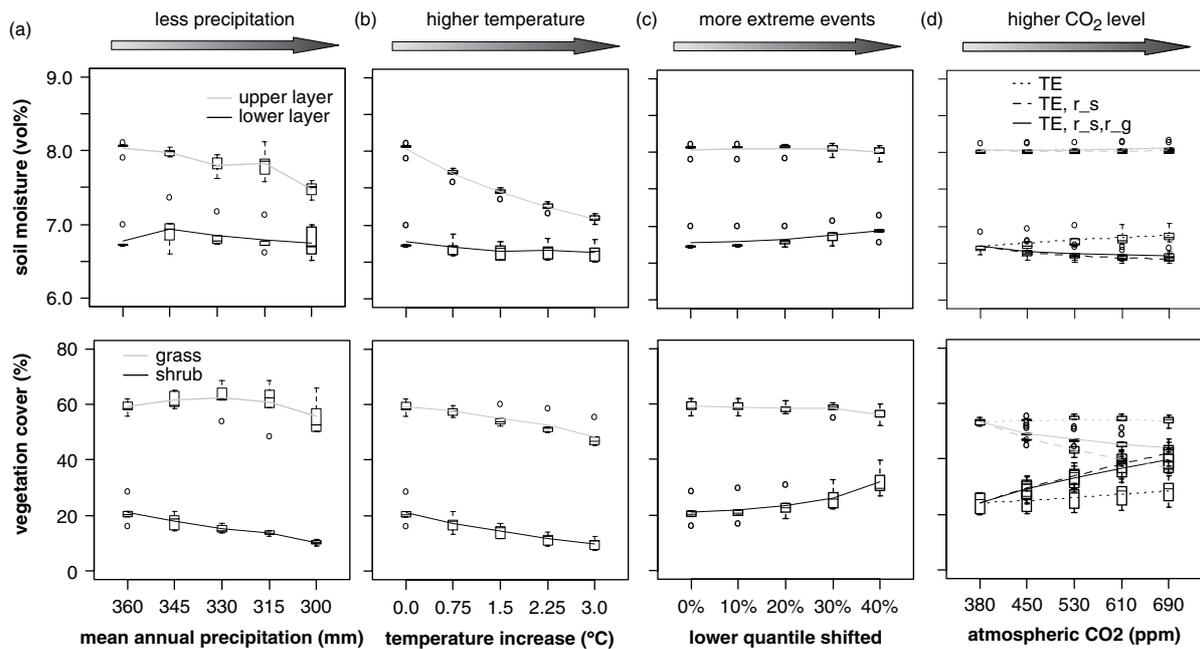

Figure 3. Effects of climatic change parameters on soil moisture and vegetation cover (box plots on simulated years 81–100). Effects of (a) decrease in precipitation, (b) increase in temperature, (c) increase in extreme events, and (d) increase in atmospheric CO_2, with abbreviations TE: increased transpiration efficiency, r_s: increased growth rates of shrubs, r_g: increased growth rates of grasses.
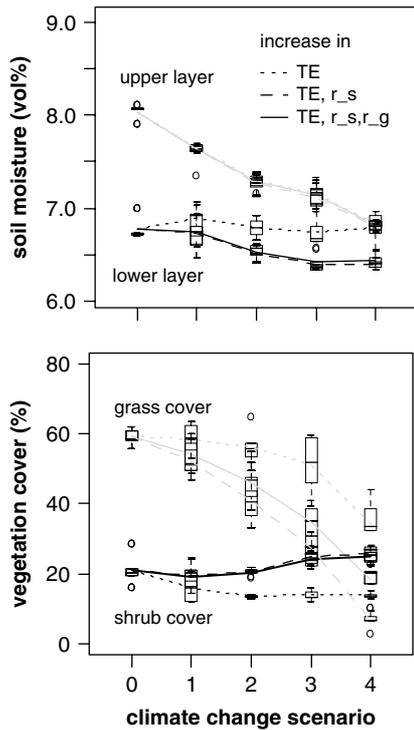
Figure 4. Combined effects of climate change on soil moisture and vegetation cover (scenarios see Tab. 3: 0 no change, and 4: the strongest change). Abbreviations: TE: increased transpiration efficiency, r_s: increased growth rates of shrubs, r_g: increased growth rates of grasses.

The combined effects of the four possible climatic changes are given in Figure 4: simulation results show decreasing soil moisture in both layers. Especially, the upper 20 cm of the soil desiccate, but also the deeper soil is considerably drier. Here, even in the wet season, mean soil moisture remains at the critical plant specific wilting points, i.e. plants close their stomata in response to water stress. The response of the two plant types to this increased stress is diametrical: while grass cover strongly declines, shrubs benefit from the reduced competitive situation. This can even shift the savanna from a grass-dominated ecosystem to a shrub-dominated system. If only transpiration efficiency is increased and growth rates of shrubs and grasses remain constant, this effect is mitigated: the decrease in grass cover is reduced, and shrubs lose their competitive advantage. In case of an additional increase in shrub growth without an increase in grass growth, the effects of climate change are exacerbated and grasses are reduced to a cover of less than 10%.

DISCUSSION

The model *EcoHyD* presents an approach of intermediate complexity, allowing for theoretical as well as applied questions. The effects of intra-annual rainfall variability as well as temperature and atmospheric CO_2 on the coupled water-vegetation dynamics can be assessed systematically. With this approach, the model differs from pure theoretical models of drylands (e.g. Rietkerk and van

de Koppel 1997; Gilad *et al.*, 2004), which are difficult to be applied to specific sites, but also from site-specific, more complex models (e.g. CENTURY model by Parton *et al.*, 1992), for which a huge parameterization effort is necessary. Although the model structure is relatively simple, overall grass cover can be reproduced realistically, as shown in Appendix A1 (supporting information).

Impacts of climate change

Understanding and predicting vegetation dynamics in drylands is of utter importance to assess the impacts of climate change on biodiversity and future land use. The model results show that the separate effects of climate change, namely changing precipitation patterns, increased temperature and an elevated atmospheric CO_2 level, can be converse. Since water is a limiting factor in drylands, a reduction in precipitation naturally has a negative effect on water availability and thus often on vegetation cover, which is adapted to specific conditions. This negative impact can be seen, although the reduction in mean precipitation is rather small compared to the present standard deviation. Also increased temperature, which is a main driver of water losses through evapotranspiration, leads to reduced water availability. In contrast, simulated soil moisture in the lower layer responds positively to an increased number of extreme events, while keeping the total annual precipitation constant. This shows that in our scenarios of more extreme events, infiltration speed is not limited by the hydraulic conductivity of the soil, and surface water can infiltrate almost completely. The pulse depth of precipitation events increases (i.e. the depth to which soil water potentials are elevated), which leads to a decline in evaporation and vapour diffusion rate, and increased plant water uptake (Schwinning *et al.*, 2004). This is reflected by the increased cover of grasses and shrubs under the scenarios of more extreme events. However, in the case of reduced topsoil hydraulic conductivity or steeper slopes, the effect of higher rainfall variability could be reverse: pronounced run-off would lead to decreased water availability and thus to a reduced vegetation cover. This is supported by findings of scenarios with a more pronounced (but unrealistic) shift to extreme events. Here, run-off increases and as a result water availability to plants decreases.

Plants can strongly differ in their response to an increased atmospheric CO_2 level and predicting this response not only on the species but on a plant type level is a future challenge (Körner, 2000). Numerous studies report the occurrence of the indirect effect of increased water use efficiency, i.e. decreased transpiration by reduced stomatal conductance (e.g. Bazzaz, 1990; Hughes, 2003; Kirschbaum, 2004; Körner, 2006). Additionally, an increased photosynthetic rate as a direct effect of higher CO_2 levels and a resulting higher dry matter production are revealed, but with a differing order of magnitude for different plant types. We met this uncertainty in plant type response by evaluating three possible CO_2 scenarios, which cover a broad range of potential

responses. Our results show that generally shrub species benefit to a higher extent from an elevated atmospheric CO_2 level than grasses. Increasing solely the water use efficiency of plants leads only to a slight increase in shrub cover. But as soon as the growth rates are also affected, shrub cover increases stronger and suppresses grass growth. These results are in good agreement with other studies (e.g. Campbell *et al.*, 2000); therefore we are positive that the model is able to capture the general response trend.

The results of the separate changes in drivers show that two main factors play a major role in the course of climate change: first, altered water availability in different soil depths; and second, a change in water allocation to a specific plant type, i.e. an altered competitive strength of plant types. These factors interact, and dependent on the intensity and nature of the change in climate drivers, one factor can prevail over the other. This and the non-linear response of the system towards changes become also apparent in the evaluation of the combined effects of the four drivers. Under present conditions, grass dominates over shrubs. If soil moisture decreases as a result of climate change, grass and shrub cover decline because of changed water availability. However, if climate change becomes more intense, the second factor comes into play and grasses lose their competitive strength. As a result, shrub cover starts to increase despite the reduced water availability. The simulated lower vegetation cover, in turn, feeds back on soil moisture dynamics: infiltration decreases and the soil moisture level declines.

Our assessment of the combined effects of different climatic changes is of course just an example of how future conditions could be. Climate change will impact regions quite differently, e.g. MAP can decrease in some regions but can increase in others (IPCC, 2007). Therefore, a tool like our model *EcoHyD*, which disentangles the separate factors of climate change, is needed to assess the future state of savannas and the conditions for land use. But our results also show that looking only at a single aspect of climate change, as it is done in many present models of dryland dynamics, which generally aggregate precipitation to annual water availability (see recent review of Tietjen *et al.*, 2007), is not adequate to assess future conditions. In our example of a Namibian thorn bush savanna, especially shrubs respond negatively to decreased precipitation, and their cover declines. However, if decreased precipitation is combined with other changes, this prediction is not reliable any longer: the ratio of shrubs and grasses alters strongly, leading to a shift from a grass-dominated ecosystem to a highly shrub-encroached system.

The model exhibits strong feedbacks between water availability and vegetation. Adaptive mechanisms such as adjustments in the vertical root distribution (Schymanski *et al.*, 2008), or evolutionary responses (Jump and Peñuelas, 2005) could mitigate some of the negative effects of decreased water availability on vegetation cover. On the other hand, in the long-term, changes in vegetation feedback not only on soil moisture, but also

on local to large-scale climate conditions. For example, changes in plant cover lead to an altered albedo and transpiration, and thus to changes in temperature and air humidity. Since accounting for these feedbacks would necessitate a full coupling with a dynamic circulation model, we assumed climate as an extrinsic factor.

Implications for biodiversity and land use

The shift from a grass-dominated system towards a highly shrub encroached system has strong implications for biodiversity, ecosystem stability and potential land use (Cingolani *et al.*, 2005). A reduction in biodiversity encompasses both: losses in species diversity and structural diversity. Of course, species diversity has an intrinsic value itself. But it is additionally closely linked to ecosystem stability and ecosystem processes (Watkinson *et al.*, 2001). That is, if biodiversity is lost in savannas due to shrub encroachment, the system can lose its stability, and degradation gets more likely. Losses in structural diversity emerge since structural diversity in arid and semi-arid savannas is mainly determined by woody vegetation (Tews *et al.*, 2004). This has also been reported to affect animal species diversity (e.g. birds: Dean, *et al.*, 1999; rodents: Blaum *et al.*, 2007a; reptiles: Wasiolka *et al.*, 2009; small carnivores: Blaum *et al.*, 2007b).

A shift in the ratio of grass to shrub cover also leads to altered fire intensity and return intervals. Although at our study site fire plays only a marginal role, in mesic savannas fire can occur at intervals as short as 1–3 years (Bond *et al.*, 2000), if enough fuel is provided by herbaceous species. These frequent fires benefit grasses, since the recruitment of mature woody plants is suppressed (Jeltsch *et al.*, 1999; Jeltsch *et al.*, 2000; Roques *et al.*, 2001). If grass cover and thus the fuel load are reduced in the course of climate change, further woody plant encroachment can be rapid (Archer *et al.*, 1995).

Furthermore, shrub encroachment and the loss of perennials strongly reduce the carrying capacity of rangelands for livestock (Perrings *et al.*, 1997). This will intensify difficulties in land management, since livestock grazing itself has led to landscapes dominated by unpalatable shrubs (Anderies *et al.*, 2002). That is, future stocking rates have to be significantly lower, or cost- or labour-intensive management activities such as woodcutting or bush fires have to be applied. Thus, it is essential to quantify the combined impacts of land use and climate change, and to evaluate different management strategies. There are a great number of models simulating livestock grazing in savannas (see a recent review by Tietjen *et al.*, 2007). However, these models do not go into the complex changes that we have to expect in future. These shortcomings should be a focus of future research, i.e. hydrology should be incorporated to a greater extent, and research on the impacts of CO_2 on savanna systems should be intensified. This work provides a first step towards this direction, and we showed that evaluating the effects of climate change implies more than accounting for reduced

MAP. A future task will be to combine this approach with livestock grazing scenarios to assess future conditions for land use.

CONCLUSIONS

To face future threats of climate change on savanna systems, it is essential to understand the underlying coupled dynamics of water and vegetation. We have shown that the change of climate factors, namely altered precipitation patterns, increased temperature and elevated atmospheric CO_2, lead to different responses of grass and shrub cover. A tool like our ecohydrological model *EcoHyD* is useful to disentangle these responses and to identify potential response patterns. At the same time, the combined effects of climate change can be assessed with the model to evaluate for example future conditions for land use. In our scenario of combined changes, we found a shift from a grass-dominated system to a shrub encroached state. We therefore conclude that climate change will exacerbate the difficulties in land use by livestock grazing, which on its own has led to heavy shrub encroachment in the past.

REFERENCES

Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist* **165**: 351–371.

Anderies JM, Janssen MA, Walker BH. 2002. Grazing Management, Resilience, and the Dynamics of a Fire-driven Rangeland System. *Ecosystems* **5**: 23–44.

Anderson LJ, Maherali H, Johnson HB, Polley HW, Jackson RB. 2001. Gas exchange and photosynthetic acclimation over subambient to elevated CO_2 in a C_3-C_4 grassland. *Global Change Biology* **7**: 693–707.

Archer S, Schimel DS, Holland EA. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2. *Climatic Change* **29**: 91–99.

Bai J, Deng W, Cui B, Ouyang H. 2007. Water diffusion coefficients of horizontal soil columns from natural saline-alkaline wetlands in a semiarid area. *Eurasian Soil Science* **40**: 660–664.

Baudena M, Boni G, Ferraris L, von Hardenberg J, Provenzale A. 2007. Vegetation response to rainfall intermittency in drylands: Results from a simple ecohydrological box model. *Advances in Water Resources* **30**: 1320–1328.

Bazzaz FA. 1990. The Response of Natural Ecosystems to the Rising Global CO_2 Levels. *Annual Review of Ecology and Systematics* **21**: 167–196.

Beatley JC. 1974. Phenological Events and Their Environmental Triggers in Mojave-Desert Ecosystems. *Ecology* **55**: 856–863.

Bertness MD, Callaway R. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* **9**: 191–193.

Blaum N, Rossmanith E, Jeltsch F. 2007a. Land use affects rodent communities in Kalahari savannah rangelands. *African Journal of Ecology* **45**: 189–195.

Blaum N, Rossmanith E, Schwager M, Jeltsch F. 2007b. Responses of mammalian carnivores to land use in arid savanna rangelands. *Basic and Applied Ecology* **8**: 552–564.

Bond WJ, Midgley GF. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 865–869.

Bond WJ, Midgley GF, Woodward FI. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973–982.

Callaway RM, Walker LR. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology* **78**: 1958–1965.

Campbell BD, Stafford Smith DM. 2000. A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. *Agriculture Ecosystems & Environment* **82**: 39–55.

Cingolani AM, Noy-Meir I, Diaz S. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecological Applications* **15**(2): 757–773.

Dean WRJ, Milton SJ, Jeltsch F. 1999. Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments* **41**: 61–78.

Dore MHI. 2005. Climate change and changes in global precipitation patterns: What do we know?. *Environment International* **31**: 1167–1181.

Drake BG, Gonzàlez-Meler MA, Long SP. 1997. More efficient plants: A consequence of rising atmospheric CO_2?. *Annual Review of Plant Physiology and Plant Molecular Biology* **48**: 609–639.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000. Climate extremes: Observations, modeling, and impacts. *Science* **289**: 2068–2074.

Fravolini A, Hultine KR, Brugnoli E, Gazal R, English NB, Williams DG. 2005. Precipitation pulse use by an invasive woody legume: the role of soil texture and pulse size. *Oecologia* **144**: 618–627.

Gilad E, von Hardenberg J, Provenzale A, Shachak M, Meron E. 2004. Ecosystem engineers: from pattern formation to habitat creation *Physical Review Letters* **93**: 098105.

Higgins SI, Kantelhardt J, Scheiter S, Boerner J. 2007. Sustainable management of extensively managed savanna rangelands. *Ecological Economics* **62**: 102–114.

Hughes L. 2003. Climate change and Australia: Trends, projections and impacts. *Austral Ecology* **28**: 423–443.

IPCC WG I. 2007. Working Group I Report "The Physical Science Basis". Pages on Climate Change, Intergovernmental Panel, IPCC Third Assessment Report: Climate Change 2001. Geneva: Intergovernmental Panel on Climate Change.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389–411.

Jeltsch F, Milton SJ, Dean WRJ, van Rooyen N. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* **84**: 583–595.

Jeltsch F, Milton SJ, Dean WRJ, van Rooyen N. 1997. Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. *Journal of Applied Ecology* **34**: 1497–1508.

Jeltsch F, Milton SJ, Dean WRJ, van Rooyen N, Moloney KA. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**: 780–793.

Jeltsch F, Moloney K, Milton SJ. 1999. Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. *OIKOS* **85**: 451–466.

Jeltsch F, Weber GE, Grimm V. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* **161**: 171.

Jump AS, Peñuelas J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* **8**: 1010–1020.

Kefi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, de Ruiter PC. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* **449**: 213–2U5.

Kirschbaum MUF. 2004. Direct and Indirect Climate Change Effects on Photosynthesis and Transpiration. *Plant Biology* **6**: 242–253.

Klausmeier CA. 1999. Regular and Irregular Patterns in Semiarid Vegetation. *Science* **284**: 1826–1828.

Köchy M. 2006. Stochastic time series of daily precipitation for the interior of Israel. *Israel Journal of Earth Science* **55**: 103–109.

Körner C. 2000. Biosphere responses to CO_2 enrichment. *Ecological Applications* **10**: 1590–1619.

Körner C. 2006. Plant CO_2 responses: an issue of definition, time and resource supply. *New Phytologist* **172**: 393–411.

Morgan JA, Pataki DE, Körner C, Clark H, Grosso SJD, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, Nippert JB, Nowak RS, Parton WJ, Polley HW, Shaw MR. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO2. *Oecologia* **140**: 11–25.

Neilson RP. 1995. A Model for Predicting Continental-Scale Vegetation Distribution and Water Balance. *Ecological Applications* **5**: 362–385.

Noy-Meir I. 1973. Desert Ecosystems: Environment and Producers. *Annual Review of Ecology and Systematics* **4**: 25–51.

Parton WJ, McKeown B, Kirchner V, Ojima DS. 1992. CENTURY Users Manual. Colorado State University, NREL Publication, Fort Collins, Colorado, USA.

Perrings C, Walker BH. 1997. Biodiversity, resilience and the control of ecological-economic systems: The case of fire-driven rangelands. *Ecological Economics* **22**: 73–83.

Polley HW. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management* **50**: 562–577.

Poorter H. 1993. Interspecific Variation in the Growth-Response of Plants to An Elevated Ambient CO_2 Concentration. *Vegetatio* **104**: 77–97.

Rawls WJ, Ahuja LR, Brakensiek DL, Shirmohammadi A. 1992. Infiltration and Soil Water Movement. In *Handbook of Hydrology*, Maidment DR (ed). New York: McGraw-Hill; 5·1–5·51.

Rietkerk M, van de Koppel J. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *OIKOS* **79**: 69–76.

Roques KG, O'Connor TG, Watkinson AR. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**: 268–280.

Sala OE, Golluscio RA, Lauenroth WK, Soriano A. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* **81**: 501–505.

Sankaran M, Ratnam J, Hanan NP. 2004. Tree-grass coexistence in savannas revisited—insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* **7**: 480–490.

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Forst PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N. 2005. Determinants of woody cover in African savannas. *Nature* **438**: 846–849.

Scholes RJ, Archer SR. 1997. Tree-Grass Interactions in Savannas. *Annual Review of Ecological and Systematics* **28**: 517–544.

Schwinning S, Ehleringer JR. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* **89**: 464–480.

Schwinning S, Sala OE. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* **141**: 211–220.

Schymanski SJ, Sivapalan M, Roderick ML, Beringer J, Hutley LB. 2008. An optimality-based model of the coupled soil moisture and root dynamics. *Hydrology and Earth System Sciences* **12**: 913–932.

Sivakumar MVK, Das HP, Brunini O. 2005. Impacts of present and future climate variability and change on agriculture and forestry in the arid and semi-arid tropics. *Climatic Change* **70**: 31–72.

Stafford Smith DM. 1996. Management of rangelands: paradigms and their limits. In *The ecology and management of grazing systems*, Hodgson J, Illius AW (eds). Wallingford: CABI; 325–357.

Tews J, Blaum N, Jeltsch F. 2004. Structural and animal species diversity in arid and semi-arid savannas of the southern Kalahari. *ANNALS OF ARID ZONE* **43**: 413.

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 drylands under climate change—a generic model of two soil layers. *Water Resources Research* **45**: W01418, DOI: 10.1029/2007wr006589.

van de Koppel J, Rietkerk M. 2000. Herbivore regulation and irreversible vegetation change in semi-arid grazing systems. *OIKOS* **90**: 253–260.

van Langevelde F, van de Vijver FC, Kumar L, van de Koppel J, de Ridder N, van Andel J, Skidmore AK, Hearne JW, Stroosnijder L, Bond WJ, Prins HHT, Rietkerk M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**: 337–350.

Walker BH, Ludwig D, Holling CS, Peterman RM. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**: 473–498.

Wasiolka B, Jeltsch F, Blaum N, Henschel J. 2009. Behavioral responses of the lizard *Pedioplanis l. lineoocellata* to overgrazing. *Acta Oecologica* **35**: 157–162.

Watkinson AR, Ormerod SJ. 2001. Grasslands, grazing and biodiversity: editor's introduction. *Journal of Applied Ecology* **38**: 233–237.

Wiegand T, Milton SJ, Wissel C. 1995. A simulation-model for a shrub ecosystem in the Semiarid Karoo, South Africa. *Ecology* **76**: 2205–2221.

Witkowski ETF, Garner RD. 2000. Spatial distribution of soil seed banks of three African savanna woody species at two contrasting sites. *Plant Ecology* **149**: 91–106.