Are savannas patch-dynamic systems? A landscape model

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ABSTRACT

Savannas are ecosystems characterized by the coexistence of woody species (trees and bushes) and grasses. Given that savanna characteristics are mainly formed from competition, herbivory, fire, woodcutting, and patchy soil and precipitation characteristics, we propose a spatially explicit model to examine the effects of the above-mentioned parameters on savanna vegetation dynamics in space and time. Furthermore, we investigate the effects of the above-mentioned parameters on tree–bush–grass ratios, as well as the degrees of aggregation of tree–bush–grass biomass. We parameterized our model for an arid savanna with shallow soil depth as well as a mesic one with generally deeper and more variable soil depths. Our model was able to reproduce savanna vegetation characteristics for periods of time over 2000 years with daily updated time steps. According to our results, tree biomass was higher than bush biomass in the arid savanna but bush biomass exceeded tree and grass biomass in the simulated mesic savanna. Woody biomass increased in our simulations when the soil's porosity values were increased (mesic savanna), in combination with higher precipitation. Savanna vegetation varied from open savanna to woodland and back to open savanna again. Vegetation cycles varied over ~300-year cycles in the arid and ~220-year cycles in the mesic-simulated savanna. Autocorrelation values indicated that there are both temporal and spatial vegetation cycles. Our model indicated cycling savanna vegetation at the landscape scale, cycles in cells, and patchiness, i.e. patch dynamics.

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1. Introduction

Savannas are ecosystems characterized by the coexistence of woody species (trees and bushes) and grasses (Scholes and Archer, 1997). The ratio between grass and woody vegetation as well as the total aboveground biomass characterizes the phases of savanna. Theoretically, tree–grass coexistence is possible if competition within life forms (tree–grass) is stronger than competition between life forms (Scholes and Archer, 1997). In savannas, usually the limiting factors to total aboveground green biomass are soil moisture and nutrient availability (Scholes and Archer, 1997). Savannas have annual precipitation that can vary from as little as 100 mm per year to 1300 mm per year (Belsky, 1990; Wiegand et al., 2006). Rain has a high degree of patchiness in time and space (Zucchini et al., 1992; Ward et al., 2004; Ward, 2009). Germination and seedling

survival of trees and bushes depends mainly on soil moisture, making recruitment episodic and rare (Sy et al., 2001; Barnes, 2001a). Thus, soil moisture is a key factor for savanna vegetation (Laio et al., 2002). Soil moisture is mainly a function of rainfall and soil properties such as porosity, water-holding capacity and soil depth (Rodriguez-Iturbe et al., 2001a,b; Fernandez-Illescas et al., 2001). These soil properties are patchily distributed within the savanna landscape (Scholes, 1990).

Fire plays an important but unclear role in savanna ecology because there are several contradictory studies on the effect of fire on savanna vegetation (Higgins et al., 2000; Russell-Smith et al., 2003). Even though fire has been proposed as a factor explaining tree–grass coexistence in savannas, the general applicability of these results is questionable. In arid savannas, the grass fuel load is often too low to support fires (Bond and Midgley, 1995; Ward, 2005; Meyer et al., 2005). Grazing, browsing, and woodcutting play an important role in savannas because selective suppression of some species favours the dominance of other species (Walker et al., 1987; Shipley et al., 1999). Furthermore, megaherbivores such as elephants and giraffes have been shown to be significant modifiers of woody–grass composition (Bond and Loffell, 2001). The effects of megaherbivores are reported to be more profound in

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savannas receiving mean annual precipitation >650 mm (Walker, 1993; Sankaran et al., 2005).

Woody invasion, i.e. the increased dominance of woody species, often unpalatable to livestock, reduces livestock carrying capacity and biodiversity of savannas and is a widespread economic and ecological problem (Moleele et al., 2002). Woody invasion is a phenomenon observed in African (O'Connor and Crow, 2000) as well as in American (Archer, 1989) and Australian (Burrows et al., 1990) savannas. The causes of woody invasion (in South Africa often referred as "bush encroachment", or shrub invasion in the US) are poorly known (Ward, 2005). There are several studies attempting to explain the phenomenon (e.g. Walker and Langridge, 1996, 1997; Polley et al., 2002; Ward, 2005; Bond et al., 2003). Management techniques to prevent bush encroachment have been proposed (e.g. Winter, 1990). The techniques proposed focus mainly on grazing intensity and fire. However, given that savanna soil and vegetation cycles outlive researchers (Bernhard-Reverserat, 1982) it is difficult to follow savanna landscape patterns and vegetation composition in the field. Therefore, modelling is a useful tool for predicting future scenarios.

Much of the difficulty in savanna modelling and management arises from dealing with very different scales in time, space, and species interactions (see e.g. Wiegand et al., 2006). Multiple spatial scales are particularly difficult to address using differential equations, because these models focus mainly on population dynamics but not on their spatial distribution. An alternative approach is to focus on the spatial distribution of trees, grass, and bushes, and to develop models which focus on the factors affecting their growth based on their neighbouring plants, rather than trying to add interaction mechanisms to models based on more uniform population dynamics. One way to do this is by the use of grid-based simulation models. In these models, a grid of cells represents the spatial distribution of vegetation, e.g. cells may be occupied by grass, bushes, or trees (e.g. Jeltsch et al., 1996). Grid-based discrete time models depict spatial dynamics with rules describing how the occupancy of the grid cells changes from one time step to the next. In classic cellular automata, the state of each cell depends only on the content of that cell and adjoining cells during the previous time step (Wolfram, 1983; Ermentrout and Edelstein-Keshet, 1993). In contrast, in grid-based models, spatial interaction is possible on all scales.

Due to the advantages of spatially explicit models in such heterogeneous environments as savannas, savanna models are increasingly often spatial (e.g. Jeltsch et al., 1996; Higgins et al., 2000; Wiegand et al., 2006, 2008; Meyer et al., 2007b). While there are several good savanna models, there is still space for improvement as a combination of competition-based and demographic modelling approach is needed (Sankaran et al., 2004). The need for spatial models is also acknowledged (Jørgensen et al., 2008). Furthermore, most models focus either on one location exclusively, and/or they assume spatial homogeneity in terms of soil properties and moisture characteristics.

The globally reported increase of woody species in savannas (Sankaran et al., 2005), is not well understood (Ward, 2005). As a result, there is a need for a new theory explaining savanna dynamics. Recently, Gillson (2004a,b) and Wiegand et al. (2005, 2006) developed the idea that savannas are patch-dynamic systems. According to this theory, savannas are patch-dynamic systems composed of many patches in different states of transition between grassy and woody dominance. While there is evidence that savannas are patchy (Gillson, 2004a; Wiegand et al., 2005), the spatiotemporal dynamics of the patchiness might be a key to understanding tree–grass coexistence (Wiegand et al., 2006). The patch dynamics hypothesis is based on two different spatial scales, the patch scale and the landscape scale, and ultimately requires investigations at both scales (Meyer et al., 2007a). Following the results

from patch scale modelling (Meyer et al., 2007a,b), in this study, we focus on the landscape scale.

Given that a key to understanding savanna dynamics may lie in recognizing their patchiness (Wiegand et al., 2006), we propose a spatially explicit model that includes the spatial variance of precipitation and soil characteristics on large spatial scales and their effects on the patchy characteristics of aboveground biomass. The aim of this paper is to introduce the model and to investigate basic properties of the spatiotemporal vegetation dynamics exemplified by two model parameterizations, representing an arid and a mesic savanna.

2. Problem formulation

2.1. Overview

The purpose of the model is to improve our understanding of the ecology of savannas at the landscape scale. To keep things simple, we focus on two hierarchical levels: vegetation patches and the landscape. The main purpose of this model is to detect (if any) vegetation cycles in savanna ecosystems.

Based on this purpose, we used a grid-based, spatially explicit, individual-based model (Silvert, 1993) to follow the dynamics of three life forms, following trees and bushes on an individual basis and grass biomass within a cell. The model represents part of a savanna by a rectangular grid of cells. Each cell is characterized by a number of trees and bushes and grass biomass. Admittedly there is no clear definition of what a tree and a bush is, as in different areas woody species are found both as bushes as well as trees (e.g. *Acacia tortilis*, pers. obs.). In this model we define as bushes woody species that are normally multi-stemmed, their maximum height rarely exceeds 2 m and may reproduce vegetatively, such as *Acacia mellifera*. We define as trees woody species with maximum height normally exceeding 2 m and reproducing sexually (e.g. *Acacia erioloba*). Each tree and bush has a unique biomass (size) and age. Grass is characterized by grass biomass only. Additionally, each cell has a value of soil porosity and soil depth. The biomass of trees, bushes, and grass in each cell changes on a daily basis through a set of rules. These rules are the key part of the model and are intended to represent the dynamics of savanna vegetation as realistically and parsimoniously as possible.

For the simulations shown in this paper, we chose a grid (X, Y) of 100 × 100 cells. Each cell corresponds approximately to 3 km on a side, giving a total area of about 90,000 km^2. The cell is updated with a daily time step, meaning that the trees, bushes, and grass might grow on a daily basis depending on soil moisture and season of the year (seasonality). The number of simulation years (S) was 2100. The first 100-year results were omitted as the model reached a stable savanna state on average at a maximum of 100 years. In the results presented, we start numbering simulation years from year 100, the year that the model has reached a stable savanna state.

2.2. Vegetation properties

Several size-classes of bushes and trees can exist within each cell. Thus each cell represents a savanna patch even though several cells together can form larger savanna patches.

Tree and bush individuals are attributed by size and age. Grass has only size as an attribute, which corresponds to grass biomass. This rule is based on the idea that vegetation biomass is constrained by environmental conditions, predominantly rain and active soil depth (Wiegand et al., 2005). Limits to tree height and thus to tree biomass derive from hydraulic lift limits as described by Ryan and Yoder (1997) and Koch et al. (2004). Given that trees are usu-

Table 1
Summary of model input parameters and simulation values.

		Units	Arid	Mesic
General characteristics				
S	Number of simulation years	Years	2000	
X	Number of cells on X-axis	Dimensionless	100	
Y	Number of cells on Y-axis	Dimensionless	100	
Ct	Tree water-biomass-conversion-efficiency factor	10^5 g/m^2	16	
Cb	Bush water-biomass-conversion-efficiency factor	10^5 g/m^2	13	
Cg	Grass water-biomass-conversion-efficiency factor	10^5 g/m^2	7	
	Equilibration period (savanna stable state)	Years	100	
Tree and bush characteristics				
Mta	Max. tree age	Years	250	
Mba	Max. bush age	Years	80	
Mts	Max. tree size	m	14	
Mbs	Max. bush size	m	6	
Smt	Mature tree size	m	2	
Smb	Mature bush size	m	0.8	
Smg	Mature grass size	cm	25	
Temperature				
$Tmax$	Max. temperature	°C	36	34
$Tmin$	Min. temperature	°C	1	5
$Tdev$	Standard deviation of temperature	°C	20	25
Soil moisture				
Mm	Max. moisture in a cell	%	100	
Cw	Constant of water losses function	cm/°C	0.9	
n	Porosity	Dimensionless	0.07 (±0.03)	0.10 (±0.05)
Z	Soil depth	cm	10 (±5)	100 (±80)
Growth				
Gts	Beginning of tree growing season	Month	November	
Gte	End of tree growing season	Month	March	
Gbs	Beginning of bush growing season	Month	November	
Gbe	End of bush growing season	Month	March	
Ggs	Beginning of grass growing season	Month	September	
Gge	End of grass growing season	Month	March	
$Htgr$	Min. moisture needed for tree growth	%	13	
$Hbgr$	Min. moisture needed for bush growth	%	11	
$Hggr$	Min. moisture needed for grass growth	%	9	
Germination				
Gts	Beginning of tree germination period	Month	January	September
Gte	End of tree germination period	Month	March	
Gbs	Beginning of bush germination period	Month	January	September
Gbe	End of bush germination period	Month	March	
Ggs	Beginning of grass germination period	Month	September	
Gbe	End of grass germination period	Month	March	
Htg	Min. moisture needed for tree germination	%	21	
Hgg	Min. moisture needed for grass germination	%	15	
Hbg	Min. moisture needed for bush germination	%	18	
Dtg	Days with min moisture needed for tree germination	Days	5	
Dbg	Days with min moisture needed for bush germination	Days	4	
Dgg	Days with min moisture needed for grass germination	Days	3	
Competition				
Tt	Intensity of tree competition	%	0.7	0.8
Bt	Intensity of bush competition	%	0.6	0.7
Gt	Intensity of grass competition	%	0.45	0.5
Seedling mortality				
Smt	Max. tree seedling age	Years	5	
Smb	Max. bush seedling age	Years	4	
Smg	Max. grass seedling age	Months	3	
$Htss$	Min. moisture for tree seedling survival	%	10	
$Hgss$	Min. moisture for grass seedling survival	%	7	
$Hbss$	Min. moisture for bush seedling survival	%	9	
$Dtsm$	Days with min moisture needed for tree seedling mortality	Days	5	
$Dgsm$	Days with min moisture needed for grass seedling mortality	Days	3	
$Dbsm$	Days with min moisture needed for bush seedling mortality	Days	4	

Table 1 (*Continued*)

		Units	Arid	Mesic
Fire				
Fm	Mean peak period of fire gauss function	Month	June	
Fsd	Standard deviation of fire gauss function	Month	April–August	
Fsh	Sharpness of fire gauss function	Dimensionless	6	
Fire 1	Constants of fire formula	m²/g	1	
Fire 2	Constants of fire formula	1/month	0.7	
Fire 3	Constants of fire formula	Dimensionless	0.5	
Fire 4	Constants of fire formula	Dimensionless	0.5	
Fire 5	Constants of fire formula	Dimensionless	0.5	
Fi	Threshold probability of fire ignition	% (Probability)	0.6	
Frts	Min. size of fire-resistant trees	m	6	
Frbs	Min. size of fire-resistant bushes	m	4	
Grazing, browsing and woodcutting				
Nc	Number of daily tree cutting activities	Dimensionless	1	2
Ng	Number of daily grazing activities	Dimensionless	4	6
Nb	Number of daily browsing activities	Dimensionless	2	3
rt, pt	*r* and *p* values of neg. binomial tree cutting function	Dimensionless	1 and 0.2	
rg, pg	*r* and *p* values of neg. binomial grazing function	Dimensionless	1 and 0.2	
rb, pb	*r* and *p* values of neg. binomial browsing function	Dimensionless	1 and 0.2	
Xc, Yc	Centre of neg. binomial tree cutting function	Dimensionless	(10, 30)	
Xg, Yg	Centre of neg. binomial grazing function	Dimensionless	(30, 10)	
Xb, Yb	Centre of neg. binomial browsing function	Dimensionless	(40, 40)	
Rain				
R	Mean annual precipitation	mm	165	780
CS	Cloud size	%	50	50

ally much deeper-rooted than grasses or bushes, the limits to tree biomass are higher than the ones to grass and bush. Thus, the main limits are soil depth and soil moisture (partly dependent on precipitation and partly on soil properties—some soils can retain moisture longer (Rodriguez-Iturbe et al., 2001a,b; Fernandez-Illescas et al., 2001)). To make the model applicable to different environments, we have developed a formula to determine the cell's upper biomass limit. There is a within-cell limit for the total biomass of each life form (*max_tree_mass*, *max_bush_mass*, *max_grass_mass*) which depends on average annual precipitation (*R*), soil depth (*z*), and a water-biomass-conversion-efficiency factor (*Ct*, *Cb*, and *Cg* for trees, bushes, and grass, respectively).

For trees, maximum biomass on a cell is restricted by

$$max\_tree\_mass \leq Ct \times Z \times R$$

with similar equations for bushes and grass being obtained by substitution. We modelled maximum biomass in a cell using the above formula because soil depth and precipitation are usually the limiting factors in savannas (Williams et al., 1996). Maximum biomass of the three life forms is independent of each other in the above formula because in a stable savanna intra-specific competition is higher than inter-specific competition (e.g. Higgins et al., 2000). Indirect inter-specific competition is included in our model via competition for soil moisture.

Grass biomass is measured in g/m². As plant growth is size-dependent (Lieberman et al., 1985), we have applied an exponentially declining growth rate as a function of size. It is also well known that height, stem circumference, and canopy area are interrelated (Harper, 1977). Even though in our model when referring to "size" we always use biomass (g/m²), in Table 1 we list tree, bush, and grass size in terms of height (m) because it is more comprehensive for the reader.

The model does not include seed dispersal or seed longevity. We assume that given that there is sufficient soil moisture for a sufficiently long period, there will be germination (Wiegand et al., 2004). As much of the seed dispersal in savannas occurs by animals that carry seeds for long distances (Barnes, 2001b), the omission of seed dispersal is a realistic simplification. From data presented from Witkowski and Garner (2000), seed longevity in most cases is not expected to be the limiting factor for germination in such environments.

3. Rule set

The savanna model consists of modules that affect the spatially explicit population dynamics of the vegetation in each cell (Fig. 1). Soil moisture is a key variable mediating the effects of many factors and processes on vegetation dynamics. In addition, the model consists of four abiotic (temperature, rain, fire and seasonality), two biotic (grazing, browsing and woodcutting) and three life-history event modules (germination, growth and mortality; Fig. 1). In the following, we describe the rules of/for these modules. The model flow is graphically represented in Fig. 2. All the values used in the model are listed in Table 1.

3.1. Soil properties

The ecohydrological role of soil texture in water-limited environments is very important (Fernandez-Illescas et al., 2001) and soil properties are very important for savanna plants (McCown and Williams, 1990). Soil is modelled as a horizontal layer of depth *Z* (in cm) (Laio et al., 2001) and porosity *n*. Soil porosity gives a measure of the difficulty that water has to penetrate the soil and is dimensionless (Rodriguez-Iturbe et al., 2001a,b). Larger porosity values indicate that more water may enter the soil. The product of soil depth and porosity *nZ* defines the active soil depth, which is the depth available for water storage (Laio et al., 2001). Each cell has its own values of porosity and soil depth, which is kept constant during a simulation. According to Blackmore et al. (1990), vegetation patchiness follows soil patchiness. To test the effects of soil properties on savanna vegetation patchiness, we incorporated three soil property scenarios:
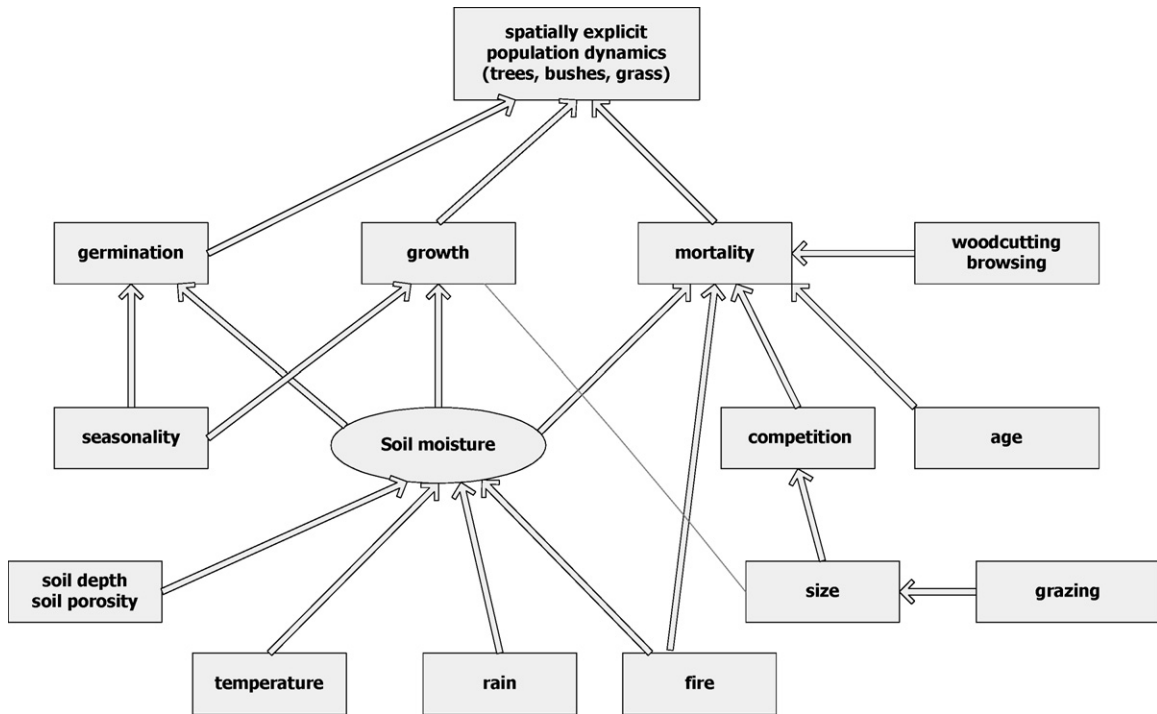
Fig. 1. Idealized spatially explicit savanna model along a soil and precipitation gradient. Size and growth are connected because they are interrelated. Arrows show influence of the starting process (box) to the one connected.

(1) Homogeneous soil layer: soil depth and porosity are identical for all cells.
(2) Patchy soil layer: each cell has porosity and soil depth values randomly distributed around a mean value of porosity and a mean value of soil depth.

(3) Soil gradient: we used a Gaussian function to generate a soil porosity gradient and a Gaussian function to generate soil depth gradient among cells. The mean value of porosity and soil depth respectively, as well as their variance and the spatial centre of the Gaussian functions are input parameters.
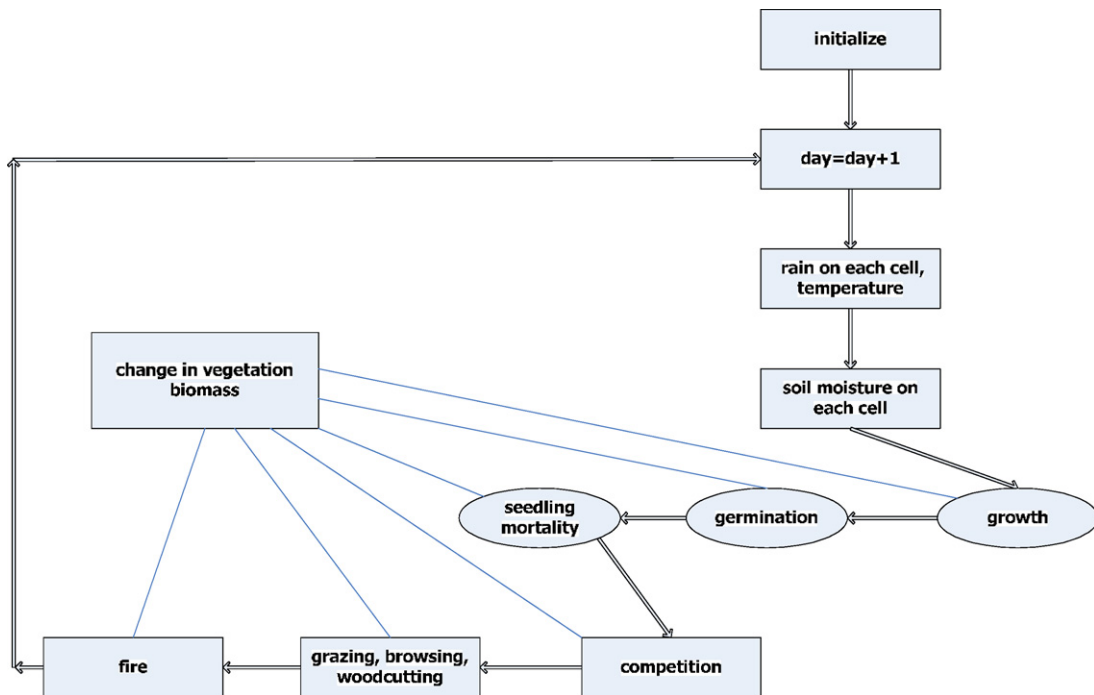

Fig. 2. Flow chart of the spatially explicit savanna model. Initialization sets the default values of soil depth, porosity and the initial values of tree, bush, and grass location, size, and age. Sequentially, for each time step (1 day), the amount of rainfall in each cell and the temperature are calculated in order to set the cell's soil moisture. Under sufficient soil moisture and during the right season, growth and germination take place. Seedling mortality occurs when soil moisture is lower than the minimum moisture needed for survival (regardless of the season). Thereafter, some mature trees, bushes and grass could die due to competition and depending upon the vegetation density. Sequentially, grazing, browsing, and woodcutting activities take place and reduce tree, bush, and grass biomass. Lastly, fire could ignite depending mainly upon grass biomass and seasonality. Fire burns all grass and all small trees and bushes in the cell.

In this paper we used patchy soil layer characteristics only. Further details on porosity and soil depth values are given in Section 6 and in Table 1.

3.2. Temperature

From data derived from the South African Weather Bureau for six different stations [data from 1940 to 2003], we heuristically found the most parsimonious function that fit these data. We found that a sinusoidal function fits the data with error that does not exceed $\pm 0.5\,^{\circ}C$. The function updates temperature on a daily basis and all cells have the same temperature during a day. The form of the above-mentioned formula is

$$Temp = Tmin + Noise + \left[(\sin(Tf + f) + 1) \times \frac{Tmax - Tmin}{2} \right]$$

where *Temp* is the current day's temperature, *Tmin* is the minimum annual temperature occurring on average in the modelled area, $Tf = (day - 1)/365 \times 2 \times \pi$, $1 \leq day \leq 365$ and $f = 0.07 - \pi/2$. The noise in temperature displacement over the year is: $Noise = U(0,1) \times Tdev - Tdev/2$, where *Tdev* is the standard deviation of the temperature through the year, and $U(0,1)$ is a random number uniformly distributed in [0,1].

3.3. Rain characteristics

Precipitation in savannas is highly variable (Williams et al., 1996). We account for this by generating daily rainfall data with different long-term mean annual precipitation (MAP) on the basis of the algorithm by Zucchini et al. (1992). Savannas with lower rainfall, however, tend to have a higher degree of rain patchiness both in space and time (Ward et al., 2004; Ward, 2009), a pattern which cannot directly be generated with Zucchini's algorithm, but does influence the vegetation structure of savannas. To allow for spatial variability in the rainfall pattern we used SERGE generator of local rainfall (Eisinger and Wiegand, 2008). SERGE is based on Zucchini's algorithm and differs from Zucchini et al. (1992) by introducing clouds of fixed sizes which resemble the spatial correlation of rainfall in a given region. As the cloud size is smaller than the area modelled, one can add additional clouds of the same storm depth but different random location until the cumulated area covered by clouds equals the size of the area modelled (Eisinger and Wiegand, 2008). Consequently, not all the simulation cells receive rain, although it does rain in the region, while some cells may receive rain twice the same day. Thus, the rainfall probabilities and the rainfall amounts are chosen in such a way that in any cell the rainfall characteristics equal Zucchini's model stochastically, though the rainfall differs between the cells on a daily basis (Eisinger and Wiegand, 2008). The MAP is a user-defined input parameter in our model, called *R*. Cloud size *CS* (the ratio of the cell covered by a cloud—see Eisinger and Wiegand, 2008 for details) was 50% for both arid and mesic-simulated savanna. The rest of the parameters used for creating rainfall are those described by Zucchini et al. (1992).

3.4. Soil moisture properties

Relative soil moisture *S* takes continuous values from [0,100] and is updated for each cell on a daily basis according to the formula:

$$S(t+1) = \frac{R(t+1) - W(t+1)}{n \times Z} + S(t), \quad 0 \leq S(t+1) \leq 100$$

where $S(t+1)$ is the cell's relative soil moisture of the current day, $S(t)$ is the cell's relative soil moisture of the previous day, $R(t+1)$ is the rain that fell on that day in the cell, *n* is soil porosity of the cell, *Z* is the soil depth of the cell and $W(t+1)$ the total water losses (leakage, transpiration, evaporation and runoff). The relative soil moisture formula was simplified from Laio et al. (2001). The major difference in our modelling approach is that we include all water losses in one factor $W(t)$ of the form:

$$W(t) = C_w TS(t)$$

where *T* is the temperature of that day, and C_w describes the water loss per $^{\circ}C$.

3.5. Fire characteristics

At a landscape level, we may assume that low intensity fires covering only a small portion of a cell do not have an important influence on the vegetation (e.g. do not change species dominance). Therefore, once a fire has started, we assume that it is strong enough to burn all grass biomass and all bushes and trees smaller than a threshold size. In addition, soil moisture of that cell is set to 0. There is a minimum fire-resistant size of trees (*Frts*) and bushes (*Frbs*).

In our modelling approach, fire ignition (*Fi*) and spread are influenced by (i) grass biomass, (ii) seasonality, (iii) soil moisture, (iv) possibly fire in a neighbouring cell (the chance increases with the number of burning neighbours), and (v) a stochastic element. On a daily basis, a randomly chosen cell is examined to determine whether it exceeds the flammability index, using the formula given below. The main fire agent is grass biomass. As dry grass burns much more easily than green grass, seasonality affects fire ignition. In order to model seasonality, we assign a Gaussian function with the peak fire likelihood located on the drier days of the year, i.e. June in our study sites. Fire is less likely to start on a humid soil surface than on a dry one. Thus, the cell's soil moisture has a negative effect on fire ignition probability. Fires are likely to spread from other burning areas, thus we examine if a neighbouring cell is already burning (from the previous time step/day). Neighbouring burning cells have a positive effect on the probability of fire ignition in that cell. Lastly, fire ignition also has an unpredictable element (anthropogenic causes, etc.). In order to account for that, we included a positive random ignition factor. After fire ignition in a cell, it is then determined if fire can spread to the eight neighbouring cells. For each cell, a flammability index *Fi* describing the probability of fire ignition is calculated and compared to a fire ignition threshold *Fi*. We also use a random number *r* uniformly distributed in [0,1] influencing fire ignition. The flammability index is

$$Fi = fire_1 \times grass\ biomass + fire_2 \times seasonality + fire_3$$
$$\times fire\ on\ neighbouring\ cell + fire_4 \times soil\ moisture + fire_5 \times r$$

Fi needed for fire ignition is an input parameter.

Long-term fire exclusion plots in savannas of various types indicate increased woody vegetation cover in sites where annual precipitation is >650 mm (Sankaran et al., 2005). In arid savannas, rainfall is too low to support fires that are intense enough to prevent the regeneration of bush from coppice (Meyer et al., 2005) and seedling growth and long-term fire suppression does not increase woody cover (Sankaran et al., 2005). In our modelling approach, we assume that although small fires exist, they are not very influential on savanna vegetation at a landscape level. Therefore, in our model, once a fire has started, we assume that it is strong enough to burn all grass biomass and all bushes and trees smaller than a certain size. The minimum fire-resistant size of trees (*Frts*) and bushes (*Frbs*), are input parameters of our model.

3.6. Seasonality

Vegetation grows exclusively during the life-form specific growth season (beginning and end date for trees: (*Gts*, *Gte*), bushes: (*Gbs*, *Gbe*), and grass: (*Ggs*, *Gge*); (Paruelo et al., 1999)). Seasonality

is an important factor for savanna plant germination (Barnes et al., 1997; Barnes, 2001a). We therefore included seasonality as an input parameter. Germination takes place exclusively during the specified season. The beginning and end of the germination season is a different pair of parameter for trees (Gts, Gte), bushes (Gbs, Gbe), and grass (Ggs, Gge).

3.7. Tree, bush, and grass growth and seedling mortality

Growth takes place only when the cell's soil moisture was above a minimum soil moisture threshold (tree: Htg, bush: Hbg and grass: Hgg) during the current day. Woody plants grow until they reach their maximum size (trees: Mts and bushes: Mbs) and thereafter do not grow any further. They die when they reach their maximum age (trees: Mta and bushes: Mba). Several savanna plants have been reported to have linear growth as a function of time (Wiegand et al., 2000). Although we use one exemplary tree and bush, our model is based on the assumption of multi-species stands and not single species stands, so our model does not account for self-thinning (but see Wiegand et al., 2008). Thus, we used a function to describe plant growth of the form:

$$tree\_mass(day + 1) = at \times tree\_mass(day) + bt$$

Growth of bushes and grass is obtained by substitution in the above formula with constant factors ab, bb for bushes and ag, bg for grass.

There are some, admittedly limited, data quantifying the longevity of perennial grass—but see O'Connor (1991). It is known that there is a time when grass will die (McCown and Williams, 1990; McKeon et al., 1990). However, it is unknown whether grass could have remained green for longer if there had been more rainfall (Burrows et al., 1990; McCown and Williams, 1990). In addition, some grass species are annual, therefore they are bound to die at the end of the season. In order to include perennial and annual grass behaviour in our model, we introduce a season where grass will die. The period through the year that grass dies is characterized by beginning and ending day. This option was deactivated in the simulations presented in this paper and thus grass is considered to be perennial.

Once germinated, tree and bush seedlings suffer high mortality (Barnes, 2001a). Therefore, when a tree is below a critical size Smt (and thus characterized as a seedling), and the soil moisture is below a minimum threshold $Htss$, during the last $Dtsm$ consecutive days for trees, the seedlings die. For example, when a tree seedling is below 2 m tall and the soil moisture during the 5 last days was lower than 10%, the tree seedlings in that cell will die (Table 1). The same procedure applies for calculating bush and grass seedling mortality with respective size values (Smb, Smg), minimum soil moisture for survival ($Hbss$, $Hgss$), and consecutive number of days ($Dbsm$, $Dgsm$). All values are listed in Table 1.

3.8. Competition—adult mortality

Competition stress is an additional source of mortality (Stoll and Weiner, 2000; Moustakas et al., 2006, 2008). The maximum biomass of trees (max_tree_mass) that can be sustained in an area of the dimension of our cell and the biomass of trees present on the cell define the competition index as

$$tree\_competition = \frac{tree\_mass}{max\_tree\_mass}$$

When $U(0,1) \times tree\_competition \geq Tt$, a mature tree (not a seedling) will be randomly killed within the cell. Note that Tt is an input parameter that defines the intensity of tree competition and $U(0,1)$ is a random number uniform in [0,1]. The above-mentioned process applies to bushes and grass according to the competition intensities Tb and Tg, respectively.

3.9. Germination

Tree and bush germination in savannas is an episodic event and the main limiting factor to this event is soil moisture (Wilson and Witkowski, 1998; Noe, 2002). Grass germination is not a rare event but has a high dependency on soil moisture (Sy et al., 2001). Germination takes place when for a number of consecutive days, a cell's soil moisture is at least equal to the minimum soil moisture needed for germination (Wilson and Witkowski, 1998). The minimum number of days and the minimum level of soil moisture needed for tree (Dtg, Htg), bush (Dbg, Hbg), and grass (Dgg, Hgg) germination are input parameters. When tree, bush, or grass seedlings reach a certain size, they are not treated as seedlings, but as mature trees, bushes, or grass, respectively. The mature tree size is Smt (Smb for bush and Smg for grass size, respectively).

The model does not include seed dispersal or seed longevity (cf. Section 2.2). We assume that, given that there is sufficient soil moisture (at the different levels that are required for trees, bushes and grass) for a sufficiently long period (different consecutive days required for each life form), there will be germination. In order to avoid unrealistic germination when there are no or few trees or bushes present (reduced seed availability), we have reduced the germination probability when the total number of trees or bushes is low. When the number of trees present is <10% of the maximum number of trees that potentially could be present in the cell, germination probability of trees is reduced by 90% (bushes and grass are treated similarly). The density-dependent germination function is active only when the above-mentioned germination criteria are fulfilled.

3.10. Grazing, browsing and woodcutting characteristics

We model the interaction of the spatial behaviour (movement) of animals in our model with grass, bushes, and trees. According to McNaughton (1985), the spatial distribution of animals is aggregated. Furthermore, grazing is more intense in places that were recently burned (Fuhlendorf and Engle, 2004) which is also an aggregated process. In addition, bushes or trees that are taller than 2 m are browsed by very few animals such as giraffe or elephants, which are mainly found in national parks. Therefore, bushes and trees over 2 m are not browsed in the model. Woodcutting usually takes place near communities or ranches rather than at large distances from them (Tobler et al., 2003). As a result, the effect of humans on woodcutting is spatially also an aggregated process with the centre of woodcutting activities defined as the centre of the inhabited area. For the above-mentioned reasons, we model grazing, browsing, and woodcutting as spatially aggregated processes. We use three negative binomial distributions, one for each process, to describe the spatial variation in grazing, browsing, and woodcutting intensity. Negative binomial distributions allow spatial aggregation. With regard to grazing, the choice of the cell that will be grazed during the following time step is non-Markovian, i.e. biased to places that were burned during the past year (Fuhlendorf and Engle, 2004; Archibald et al., 2005). The input parameters for each of the three distributions are the centre of the activity (Xc, Yc) (Xg, Yg) (Xb, Yb), the mean (rc, rg, rb) and variance (pc, pg, pb), as well as the number of activities per day (Nc for human impacts, Ng for grazing impacts, Nb for browsing impacts). For example, when the number of woodcutting activities per day Nc is set to 2, then two cells will be chosen according to the negative binomial distribution centred around (Xc, Yc) with mean rc and variance pc and trees will be killed in each cell accordingly. This assumes that the entire tree dies which might be incorrect in a few cases of trees such as *A. erioloba* where dead branches are usually lopped off by people, but it is generally a realistic assumption. Arid savannas support fewer humans and animals than mesic savannas. We

therefore assumed that numbers of daily grazing, browsing, and woodcutting activities are lower in arid savannas. The grazing centre is adjusted to fire by keeping in memory the burned cells during the past two years. The above-mentioned grazing distribution is biased by favouring 20% higher probability of grazing in cells that were burned during the last two years.

4. Initialization

Soil depth and porosity values are drawn for each cell according to the distribution chosen (constant, gradient, or Gaussian). Soil depth and porosity values, once distributed in each cell, remain constant during a simulation period. Furthermore, in each cell, a value of grass biomass as well as a number of trees and bushes is given. The size and age of each tree and grass are randomly chosen. Number of trees and bushes in a cell can never exceed the maximum number of trees and bushes in a cell, respectively. In addition, tree and bush age and size do not exceed maximum tree or bush size and age. Additionally, grass biomass distributed in each cell will not be larger than the maximum grass biomass in a cell. According to the parameterization of the model, some years of simulation are necessary for the model to generate a realistic savanna pattern. We retain statistics of tree, grass, and bush biomass after the initial simulation period (Sss), which was 100 years.

5. Output

In order to assess data on spatial statistics, we record the tree, bush, and grass biomass in each cell. During the same time interval, we also record the biomass removed due to herbivory (grazing and browsing) and woodcutting, as well as the burned tree, bush, and grass biomass in each cell. We calculate the mean and coefficient of variation of all the above-mentioned characteristics. The coefficient of variation (CV) is frequently used as an index of spatial (and temporal) size variability of individuals (Simpson et al., 1960). Similarly, applying the CV on the above-mentioned spatial attributes, one can use CV as a measure of patchiness.

Spatial autocorrelation is an appropriate index of measuring patches and gradients (Legendre, 1993). We calculate spatial autocorrelation using Moran's index (e.g. Overmars et al., 2003) in 10 user-defined cells. To detect possible cycles, we also calculated temporal autocorrelation in 10 user-defined cells every 20 years.

6. Model parameterization

We parameterized the model for two exemplary savanna systems: arid and mesic. Apart from the obvious difference of the MAP levels between the two sites, there are several other differences between arid and mesic savannas. Soil quality expressed in our model as porosity and soil depth are usually different between arid and mesic environments. Arid environments usually have shallower soil depth and porosity values—although there are counter examples of *A. erioloba*-dominated savannas in the Kalahari (Moustakas et al., 2006) or *Terminalia sericea* savannas on deep sands (Katjiua and Ward, 2006). The probability of fire is considerably lower in arid environments because there is insufficient grass fuel to support large fires (Meyer et al., 2005). Therefore, arid landscapes are less fire-driven than mesic ones. In arid environments, percentage of plant cover is low. As a result, there is less available food and generally fewer animals and a lower human population per hectare. Therefore, grazing, browsing, and woodcutting activities are less frequent (but not necessarily less intensive). Published data were used about the tree, bush and grass growing seasons (Barnes et al., 1997; Golluscio et al., 1998; Veenendaal et al., 1996).

The arid study area is located west of Windhoek on the western edge of the Khomas Hochland, Namibia on three adjacent ranches: Quabis, Tweespruit, and Changans (Ward et al., 2004). These ranches are situated between two parallel mountain ranges. There is a shallow layer of sandy soil overlying Swakop schist from the Damara sequence. Thus, roots of both woody and grassy plants are confined to a thin soil layer (<5–15 cm deep). Rain falls in summer (January–April) and is very patchy MAP = 122 mm (±50 mm). Tree and bush germination period on the area is mainly January–March, and grass germination period is September–March. Growth season for tree and bush species is mainly November–March, while for grass it is September–March. More details on the study area are given by Ward et al. (2004). A list with all the parameters used in the simulated arid savanna is given in Table 1.

The mesic study area is located on the Serengeti plains, Tanzania. We mainly focused on the area around Banagi. Rain falls mainly from November to May. Rain is patchy and highly variable through years; MAP = 780 mm (±283 mm). The area around Banagi is generally woodland, with mainly brown calcareous soils (Anderson and Talbot (1965). Minimum soil depth is 20 cm but in some places roots are still common at depths of up to 200 cm. Tree, bush, and grass germination period in the area is mainly September–March. Growth season for tree and bush species is mainly November–March, while grass growth is September–March. A detailed description of the area including tables of soil and vegetation characteristics are given by Anderson and Talbot (1965). For each of the two exemplary savanna systems we averaged results from 100 simulation runs to account for the variation among runs. A list with all the parameters used for the simulated mesic savanna is given in Table 1.

7. Results

Overall total biomass showed a cyclic behaviour through time (Figs. 3 and 4). Grass life cycle was about three years, bush life cycle was on average 50 years, and tree life cycle was on average 200 years (results not shown here). The total aboveground biomass is the combined effect of the grass, bush, and tree cycles. As a result, starting from an open savanna with scattered trees and bushes, there is a period where savanna vegetation generally decreases due to climatic variations, then there is a period when savanna becomes a woodland with further increase of woody species, and then a period where savanna becomes more open again (Figs. 3 and 4). The periodic transition from open to more encroached savanna (more woody species) was a general result for both the arid and mesic savanna (Figs. 3 and 4). However, in our simulations, the period of a cycle was ~300 years in the arid savanna and ~230 years periods in the mesic savanna (Fig. 4).

Overall, tree biomass was higher than bush biomass in the arid savanna but bush biomass exceeded tree and grass biomass in the simulated mesic savanna (Table 2). Tree biomass did not differ much between arid and mesic simulations. However, grass and bush biomass were affected by the difference in precipita-

Table 2
Mean biomass, variance and CV values of tree, bush and grass biomass, respectively.

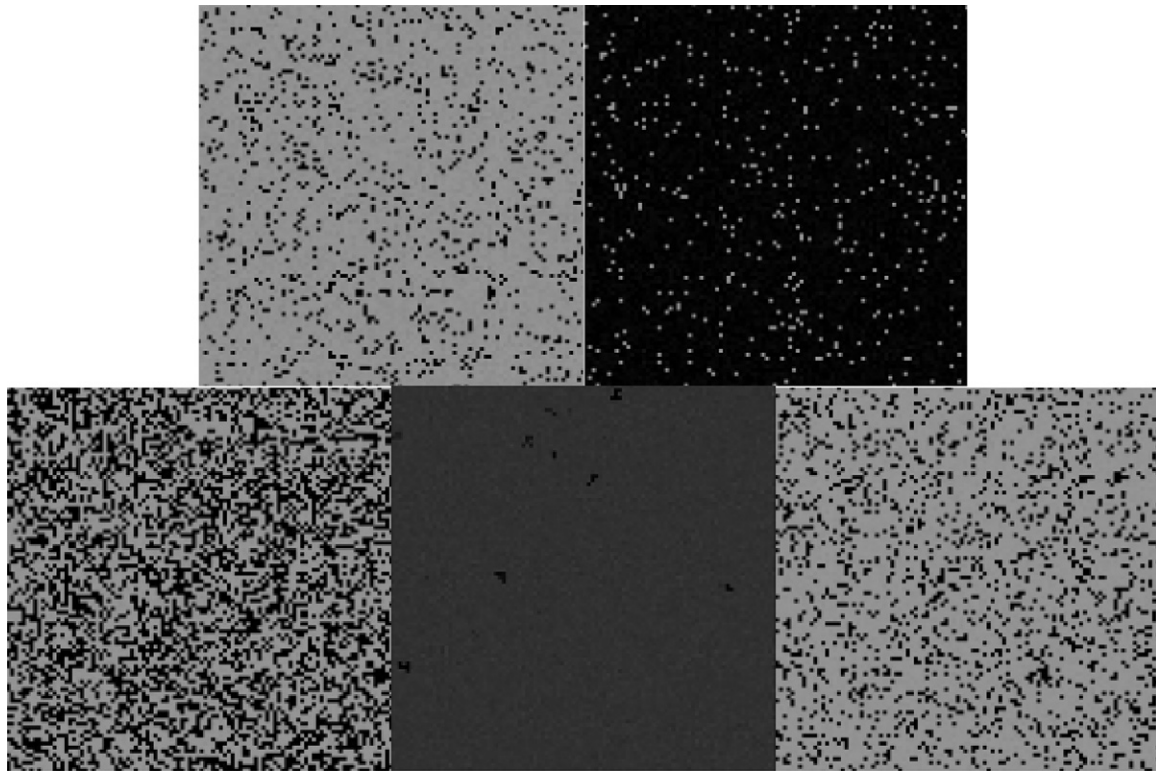|	Tree	Bush	Grass
Mean Biomass (g/m^2)			
Arid	874.2	737.7	140.6
Mesic	1074.4	1126.2	974.3
Variance (g/m^2)			
Arid	9957.1	912.7	487.6
Mesic	27374.8	46905.7	131.0
CV			
Arid	113.9	123.7	34.7
Mesic	254.8	256.8	134.5

Fig. 3. Snapshots of savanna vegetation pattern over 300-year simulation cycles. Lighter colour depicts lower biomass values. There is a periodical transition from an open savanna (upper left) to an open savanna (upper right) sequentially to a highly vegetated savanna with closely spaced vegetation (down middle), to an open savanna again (down right). The results shown here are taken from the simulation of the arid savanna. Similar cycle and pattern is observed in the simulated mesic savanna too. Snapshots shown here were taken in (years) $t = 620, 740, 800, 860$ and 920 (cf. Fig. 4).

tion. Bush biomass was almost doubled in the mesic savanna and grass biomass increased almost sevenfold as a result of precipitation variation. The CV of tree biomass was higher in the mesic savanna. Therefore, tree patches are more unpredictable in the mesic savanna. Bush biomass variance increased dramatically in the mesic savanna. However, the CV of bush biomass did not increase at the same level. Therefore, even though in the mesic savanna there were bushes in more places than in the arid savanna, patches are more unpredictable and patch size more uneven. Even though grass biomass variance decreased in the mesic savanna, grass CV increased. Therefore, grass patches in the mesic savanna had similar sizes but the degree of grass patchiness increased (Table 2).

Spatial autocorrelation, quantified using Moran's index, took both negative and positive values in the arid and mesic-simulated savannas. Overall, in both the arid and mesic savannas, Moran's index values peaked in locations (cells) located closer to each other, declining thereafter and finally peaking again at larger distances but with lower autocorrelation values than in neighbouring cells (Fig. 5a and b).

In the arid savanna, areas (cells) at distances of 30 km from each other (corresponding to 10 cells × 3 km/cell = 30 km) from each other were highly correlated. Spatial autocorrelation was still high but declined in locations at distances 60–90 km from each other (corresponding to 20–30 cells in the model) (Fig. 5a). Spatial autocorrelation was positive but negligible at distances of 120 km (40 cells) and 180 km (60 cells) and negative but negligible at distances of 150 km (50 cells). Spatial autocorrelation in the arid-simulated savanna was negative with high values at distances of 210 km and high but slightly lower at distances of 240 km (70 and 80 cells, respectively). At distances of 270 km (90 cells), spatial autocorrelation was positive but with Moran's index close to 0.4 and at distances of 300 km (100 cells) positive with low autocorrelation values (close to 0.2, Fig. 5a).

In the mesic savanna, spatial autocorrelation values were positive and peaked at distances of 30 km (10 cells). Moran's index values were still positive and high up to 90 km distances (30 cells) (Fig. 5b). Negative values, with Moran's index around −0.4 were encountered at distances of 150 and 180 km (50 and 60 cells). Spatial autocorrelation was not significant and negative at 210 and 240 km
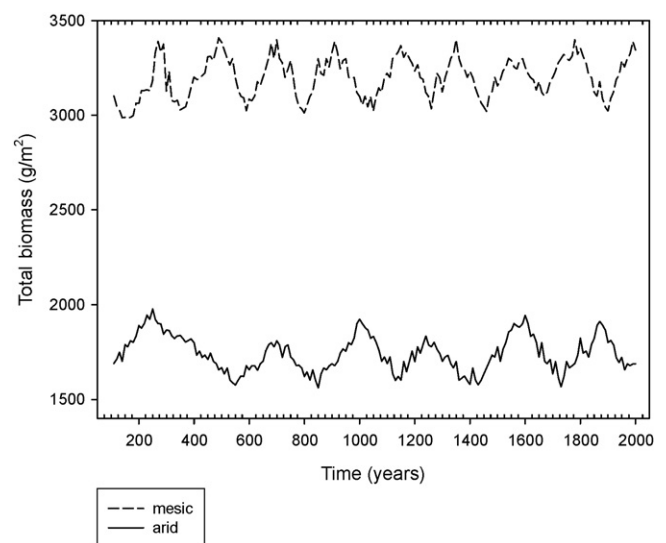

Fig. 4. Total savanna biomass (tree, bush, and grass) over 2100-year simulations. The first 100-year results were omitted as the model reached a stable savanna state on average at maximum 100 years. Results are updated every 10 years. The lines or dots connecting biomass values every 10 years, do not show intermediate biomass values; they are connected for examining trends. The biomass snapshots shown in Fig. 3 are referring to the arid savanna and taken in years 620, 740, 800, 860, 920.
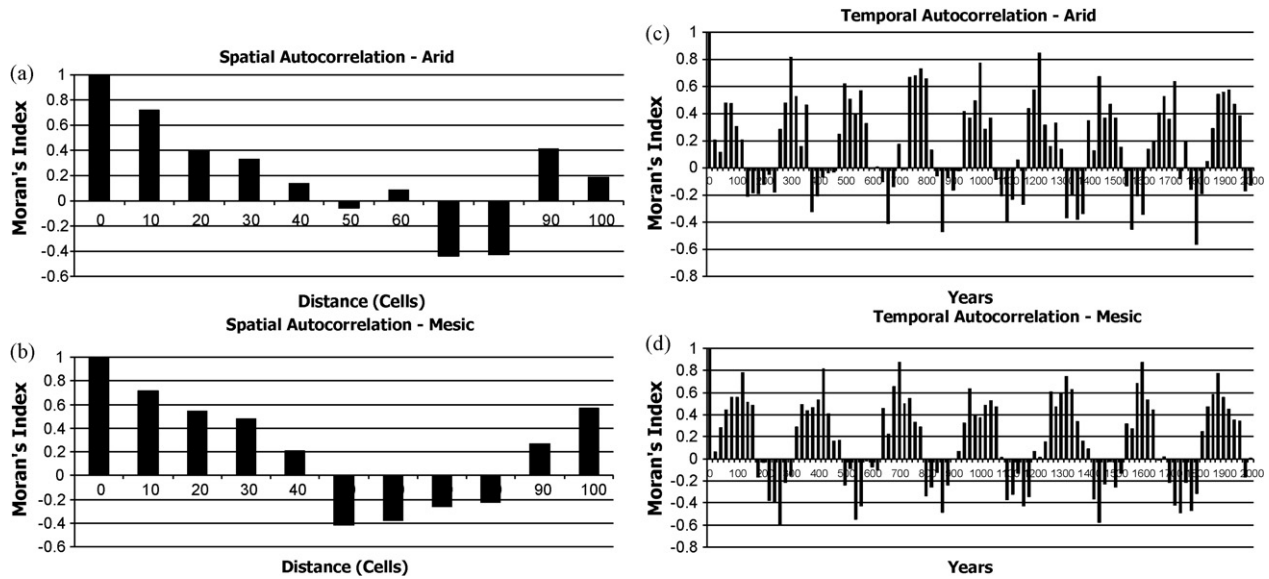
Fig. 5. Spatial and temporal autocorrelation analysis of total aboveground biomass (tree, bush, and grass biomass) for the arid and mesic-simulated savanna. Each point in the graph shows the autocorrelation values averaged over 10 selected cells. Autocorrelation values were calculated using Moran's index. Moran's index has feasible values from −1 to 1. Negative values indicate that large values are located close to small values. Positive values indicate that values of the same magnitude are located close to each other (small close to small and/or large close to large). Values close to 0 indicate no autocorrelation.

(70 and 80 cells), and not significant but positive at distances of 270 km (90 cells). Spatial autocorrelation was positive and close to 0.4 at 300 km (100 cells) (Fig. 5b).

Temporal autocorrelation values had a sinusoidal distribution with a higher turnover period in the arid savanna than in the mesic one. Temporal autocorrelation values in the arid simulated savanna were generally more variable than the ones in the mesic savanna (Fig. 5c and d).

In the arid savanna, there was a sinusoidal distribution of the Moran's index values with a period of about 230 years (Fig. 5c). Starting from a point (year) when Moran's index peaked with typical values close to 0.8, Moran's index values gradually decreased with time, taking values close to 0 after about 57 years. Moran's index took negative values, with the minimum at about 115 years (on average), values close to 0 at about 171 years, and positive values again with a peak at about 230 years. Overall, the percentage time that the autocorrelation values were positive was longer than the percentage time that the Moran's index values were negative (Fig. 5c).

In the mesic savanna there was also a sinusoidal distribution of the Moran's index values, with a period of about 300 years (Fig. 5d). Starting from a point (year) when Moran's index peaked with typical values close to 0.8, Moran's index values gradually decreased over time, taking values close to 0 after about 75 years. Moran's index took negative values with a minimum at about 115 years (on average), values close to 0 at about 225 years, and positive values again with a maximum at about 300 years. Overall, as was the case in the arid savanna, the percentage time that the autocorrelation values were positive was longer than the percentage time that the Moran's index values were negative (Fig. 5d).

8. Discussion

Our model was able to reproduce savanna vegetation characteristics for periods of time over 2000 years with daily updated time steps. Jeltsch et al. (1996), using spatially explicit simulations, found that higher rainfall increased woody recruitment and the simulated savanna turned into woodland. This result lead Jeltsch et al. (1996) to the conclusion that "factors or processes other than com-

petition for moisture, herbivory and fire are needed in addition to induce a long-term persistence of scattered trees". Using our modelling approach, increased precipitation did not turn the simulated savanna into woodland. Fire, grazing, browsing, and woodcutting are often suggested to be the main driving forces (e.g. Van de Koppel and Prins, 1998). Even though they affected patchy vegetation characteristics (results not shown here), according to our findings they were not as important in the sense that they were unable to prevent or eliminate the observed vegetation cycles. The latter is applicable for human population activities (woodcutting) too. On the other hand, our results comply with O'Connor (1993), who found that "an extrinsic force presumably rainfall had the greatest effect on population growth".

8.1. Results on a gradient basis

Our mesic savanna had, on average, higher precipitation, porosity and soil depth values than the arid savanna due to our parameterization. Woody biomass increased in our simulations when the soil's porosity values used in simulation were increased (mesic savanna), in combination with higher precipitation. Williams et al. (1996), measuring the composition and structure of tropical savannas as a function of precipitation and soil texture, found that tree height declined with decreasing rainfall, which is in agreement with our findings. In the same study, it was also found that canopy cover, and basal area of woody species declined with decreasing rainfall and increasing soil clay content. Clay has a high porosity and moisture value in comparison with other types of soil (Fernandez-Illescas et al., 2001). In our arid savanna, soil is shallow and with low porosity values, while usually the opposite is valid for our mesic-simulated savanna, even though soil properties are patchily distributed. Thus, even though our results do not indicate any necessary correlation between precipitation, porosity, and bush biomass, there were findings in common with those of Williams et al. (1996) as listed above (Table 2). In addition, according to our results, tree biomass was higher than bush biomass in the arid savanna but bush biomass exceeded tree and grass biomass in the mesic-simulated savanna (Table 2).

8.2. Comparisons with field studies

There are field studies that have already suggested that, over large scales, savannas may undergo cycles between grassland and woodland (e.g. Dublin et al., 1990), but the phenomenon of cyclical transitions was not examined across several spatial scales. Furthermore, the analogy to savanna patch dynamics at the scale of individual trees was observed by Belsky and Canham (1994). It has also been recorded that there existed an analogy of savannas with gap-demanding and shade-tolerant tree species in forests. Dominant *Acacia* species were found not to be able to recruit under themselves, but various broad-leaved shrubs (both deciduous and evergreen) did so, and thus self-thinning would occur, generating succession in species dominance in different places (Smith and Goodman, 1986, 1987). Using palaeoecological techniques to compare vegetation heterogeneity in an east African savanna over hundreds of years, it was found that patterns of vegetation change are different at the three spatial scales of observation, and suggest that different ecological processes dominate tree abundance at micro-, local and landscape scales (Gillson, 2004a). Interactions between plants, disturbance, e.g. by fire and herbivores, climate and soil type may influence tree density at differing spatial and temporal scales (Gillson, 2004a). While we are unable to directly compare the finding of cyclical transitions with periods of 220 years in mesic and 300 years in arid savannas, one may observe that the cyclical transition has been indirectly reported. However, with the exception of Gillson (2004a) it was not examined across several temporal scales.

There are also incidental observations about the variability in encroachment, along the Waterberg in north-central Namibia (near Otjiwarongo). When C.J. Andersson travelled there in the 1850s it was so encroached that it took him 3 days to travel 40 km along its length (Andersson, 1856). When the German Schutztruppe went there in the 1880s it was clear again. Today it is encroached once more (pers. obs.).

8.3. About savanna vegetation cycles

Despite the general interest in non-linear dynamics in animal populations, plant populations are often believed to show a stable equilibrium. However, the existence of possible vegetation cycles may have been overlooked because empirical studies usually are too short and most modelling studies ignore important spatial aspects of local competition and establishment (Bauer et al., 2002). However, there are several cases of cyclical transitions observed in different ecosystems (Loreau, 1997; Bauer et al., 2002; Crespi, 2004), including savannas (Gillson, 2004b; Wiegand et al., 2005). Our simulation results here showed vegetation cycles in the two exemplary savanna ecosystems that our model was calibrated for. Temporal vegetation cycles in the simulations are found in the total aboveground biomass (Figs. 3, 4, and 5a and b). Spatial vegetation cycles are found also in the total aboveground biomass, which was confirmed by the spatial autocorrelation values (Fig. 5c and d). Using Moran's index, we showed a sinusoidal behaviour both in time and space. Typically, values close to 0 show no spatial autocorrelation. Values of Moran's index close to 1 showed that patches with low vegetation are located close to patches with low vegetation and highly vegetated patches were located close to highly vegetated patches at a significant level. Values of Moran's index close to −1 showed that highly vegetated patches are significantly located close to open patches. Our results show that spatially (i.e. no time replicate) there are patches containing increased levels of woody species located close to other patches containing increased levels of woody species and open patches are closely located to open patches (high autocorrelation values). At intermediate distances, patches had lower similarities (different vegetation and different

tree–grass ratio), meaning that at intermediate distances there were both open and encroached patches. As distance between the examined patches increased again, similarity of patches increased. Spatial and temporal autocorrelation values do not necessarily offer causality of patch dynamics; however they offer strong inference of patch dynamics. Evidence of patch dynamics in savannas may be verified when other potential causes of spatiotemporal autocorrelation have been excluded.

At a temporal scale (examining a specific savanna patch over time) the patch passes through a cyclical transition from open savanna to woodland (increased levels of woody species) and back to an open savanna again. This is supported by the fact that the patch in a short time frame has similar and positive autocorrelation values, meaning that if the patch was encroached or an open savanna it remains so. As time passes, autocorrelation values became negative, meaning that encroached patches became open and open patches increased in woody vegetation, and finally after 230 years for arid savannas and 300 years for mesic ones, the patch returned to the state that occurred when the simulation started.

The fact that we found a periodicity in savanna vegetation dynamics supports the hypothesis that savannas are patch-dynamic systems (Gillson, 2004a; Wiegand et al., 2006) with bush encroachment as an integral part of their dynamics (Wiegand et al., 2006; Meyer et al., 2007a). According to our results, there is spatial and temporal variation of the savanna vegetation. Temporally, a patch will pass through an encroached phase and sequentially to a more open savanna, until it is encroached again (and *vice versa*). Spatially, when a savanna is viewed at a specific time step, there are some encroached patches, while some other patches are open savanna. Furthermore, our finding that tree and bush patches were similar at larger than intermediate distances, implies that some parts of a savanna always contain some patches with increased woody species biomass. In that case, we will have to accept that there will always be some bush encroachment. Management measures recommending altered grazing frequency and intensity (e.g. McKeon et al., 1990; Moleele et al., 2002) or changes in fire regimes should not aim to completely eradicate bush encroachment unless we want to destroy savanna systems, turning them into pure grasslands for pastoral use.

It is frequently reported that savanna nutrients are characterized by cycles (Bernhard-Reverserat, 1982; Boutton et al., 1999). Recently, tree spacing cycles in a savanna ecosystem were also reported (Moustakas et al., 2008). Our results imply that there are also vegetation cycles. If the existence of vegetation cycles is valid, then the interpretation of vegetation changes and management should take these cycles into account. Thus, management measures will have to be developed that contain bush encroachment at its natural level, which ensures that there are some patches of bush encroachment (good for the future state of the savanna), but not too many (good for livestock). Furthermore, one may want to reduce patches of bush encroachment to a point that conserves the positive effect of nutrient enrichment by encroaching trees but reduces suppression of grasses due to competition for water. Using a grid-based model of savanna vegetation dynamics in the Kalahari, Jeltsch et al. (1997) concluded that, although the stocking rates recommended by pasture scientists are unlikely to lead to shrub encroachment within 20 years, they have a high probability of bringing about shrub encroachment within a century. According to our findings, there is no way of avoiding shrub encroachment within a maximum of 200 years.

8.4. Comparison with results on a patch scale

We modelled savannas using a grid-based, object-oriented, spatially explicit model. The scale used was 3 km on a side of each cell and a grid of 100 × 100 cells, resulting in a total area

of about 90,000 km^2. Results from a grid-based, object-oriented spatially explicit model on a finer scale (within the patch scale) used by Meyer et al. (2007a) indicated significant positive auto-correlation with a temporal scale of about 33 years. The grid size used was 10 cm on a side (512×512 cells) covering in total an area of 51.2 m^2 (Meyer et al., 2007b). Thus, both at the fine scale (within the patch) as well as at a landscape level (several patches), modelling results have shown evidence of savanna patch-dynamic behaviour. According to our results presented here, total aboveground biomass has different periods of vegetation cycles; vegetation turnover periods are shorter in the mesic-simulated savanna than in the arid one, with periods of around 220 and 300 years, respectively. The savanna modelling results presented here were calibrated for an arid savanna with MAP = 165 mm and a mesic one with MAP = 780 mm. Results from SATCHMO (Meyer et al., 2007b), were calibrated for a study area where MAP = 377 mm. Combining the findings from a fine scale (within the patch) and landscape (several patches), savanna ecosystems can be viewed as patch-dynamic systems, with patches rotating at different hierarchical levels, as suggested by Gillson (2004a) and Wiegand et al. (2006). This finding may not be applicable in humid savannas as maximum aboveground vegetation is not reported to be precipitation driven (Sankaran et al., 2005). However, the fact that the aboveground vegetation was not found to be precipitation driven, does not necessarily imply that there are no cycling patches formed, as the latter was not examined in the 854 field sites investigated by Sankaran et al. (2005). It is more unlikely though to find cycling patches as the percentage of vegetation cover increases, because high precipitation may increase total aboveground vegetation to a point that there is a more continuous vegetation layer (though discontinuous enough for an ecosystem to be characterized as savanna).

Acknowledgements

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