



# Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning

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In this paper, we address the question whether and through which mechanisms herbivores can induce spatial patterning in savanna vegetation, and how the role of herbivory as a determinant of vegetation patterning changes with herbivore density and the pre-existing pattern of vegetation. We thereto developed a spatially explicit simulation model, including growth of grasses and trees, vertical zonation of browseable biomass, and spatially explicit foraging by grazers and browsers. We show that herbivores can induce vegetation patterning when two key assumptions are fulfilled. First, herbivores have to increase the attractiveness of a site while foraging so that they will revisit this site, e.g. through an increased availability or quality of forage. Second, foraging should be spatially explicit, e.g. when foraging at a site influences vegetation at larger spatial scales or when vegetation at larger spatial scales influences the selection and utilisation of a site. The interaction between these two assumptions proved to be crucial for herbivores to produce spatial vegetation patterns, but then only at low to intermediate herbivore densities. High herbivore densities result in homogenisation of vegetation. Furthermore, our model shows that the pre-existing spatial pattern in vegetation influences the process of vegetation patterning through herbivory. However, this influence decreases when the heterogeneity and dominant scale of the initial vegetation decreases. Hence, the level of adherence of the herbivores to forage in pre-existing patches increases when these pre-existing patches increase in size and when the level of vegetation heterogeneity increases. The findings presented in this paper, and critical experimentation of their ecological validity, will increase our understanding of vegetation patterning in savanna ecosystems, and the role of plant–herbivore interactions therein.

Savanna ecosystems, characterised by a continuous layer of grass intermixed with a discontinuous layer of trees and shrubs, are among the most striking vegetation types where contrasting plant life forms co-dominate (Scholes and Archer 1997). Factors regulating the balance between these life forms include rainfall, soil type, disturbances (e.g. herbivory and fire) and their interactions (Greig-Smith 1979, Huntley and Walker 1982, Archer 1990, Scholes and Walker 1993). Savanna vegetation is spatially heterogeneous and often shows patterning, frequently a two-phase pattern of discrete shrub or tree clusters scattered throughout grassland (Archer et al. 1988, Archer 1990, Couteron and Kokou 1997, Breshears 2006). Understanding the origin of such vegetation patterns is a central issue in ecology (Greig-Smith 1979, Jeltsch et al. 1996, Sankaran et al. 2004, 2005), for vegetation patterning can have important consequences for ecosystem functioning (Adler et al. 2001, Rietkerk et al. 2004). At broad spatial scales, the key determinants of patterning in savanna vegetation include spatial differences in abiotic characteristics such as rainfall and nutrient availability (Greig-Smith 1979, Hunt-

ley and Walker 1982, Scholes and Walker 1993). On the other hand, herbivory, fire, surface-water run-on and run-off processes and soil nutrient-organic matter dynamics are considered as important determinants of vegetation patterning at finer scales (Greig-Smith 1979, Huntley and Walker 1982, Scholes and Walker 1993, Jeltsch et al. 1996, 1998, Van de Koppel and Prins 1998, Klausmeier 1999, HilleRisLambers et al. 2001, Lejeune et al. 2002, Sankaran et al. 2004, 2005). However, the mechanisms behind spatial vegetation patterning in savannas are still poorly understood (Jeltsch et al. 2000, Weber and Jeltsch 2000, Sankaran et al. 2004, 2005).

Albeit several mechanisms underlying patterning in savanna vegetation have been proposed (e.g. diffusion driven instabilities: Rietkerk et al. 2002, 2004, Kéfi et al. 2007, Scanlon et al. 2007, and disturbance by fire: Van de Vijver 1999, Van Langevelde et al. 2003), the potential influence of herbivores on the spatial component of savanna vegetation remains obscure (Scholes and Archer 1997, Jeltsch et al. 2000, Weber and Jeltsch 2000, Lejeune et al. 2002, Sankaran et al. 2004, 2005). Since savannas support a

Table 1. Parameters used in the model and their interpretation.

Name	Interpretation	Units	Values	Sources
$w_{in}$	Annual amount of infiltrated water	$\text{mm m}^{-2} \text{yr}^{-1}$	560	
$\alpha$	Proportion of excess water that percolates to the tree root zone	–	0.4	De Ridder and Van Keulen (1995)
$\beta$	Soil moisture content in the grass root zone above which water starts to percolate to the tree root zone	$\text{mm m}^{-2} \text{yr}^{-1}$	350	De Ridder and Van Keulen (1995)
$r_H$	Water use efficiency of grass biomass	$\text{g mm}^{-1}$	1	Gambiza et al. (2000)
$\theta_H$	Rate of water uptake per unit grass biomass	$\text{mm m}^{-2} \text{g}^{-1}$	0.9	Walker et al. (1981)
$\theta_W$	Rate of water uptake per unit woody biomass	$\text{mm yr}^{-1} \text{g}^{-1}$	0.5	Walker et al. (1981)
$d_H$	Specific loss of grass biomass due to mortality	$\text{yr}^{-1}$	0.9	Gambiza et al. (2000)
$r_W$	Water use efficiency of woody biomass	$\text{g mm}^{-1}$	0.5	Le Houérou (1980)
$d_W$	Specific loss of woody biomass due to mortality	$\text{yr}^{-1}$	0.4	Le Houérou (1980)
$h_t$	Total height	m	0.5–10	
$h_b$	Canopy bottom height	m	$1/3 h_t$	
$h_m$	Canopy midpoint height	m	$2/3 h_t$	
$c_w$	Canopy width	m	$3/4 h_t$	
$I_{in}$	Index value for the incident light intensity above the canopy	–	1	
$k$	Light extinction coefficient of browseable biomass	–	0.2	Huisman et al. (1997)
$f_d$	Yearly food intake as proportion of body mass	–	9.125	Owen-Smith (2002)
$G$	Grazer density	$\text{g m}^{-2}$	1.0	
$B$	Browser density	$\text{g m}^{-2}$	0.1	
$\lambda$	Amount of forage removed by the herbivores from a selected cell in each iteration of the foraging loop	g	500	
$i_{max}$	Maximum food intake rate at high food abundance	$\text{g min}^{-1}$	20	Owen-Smith (2002)
$g_{1/2}$	Food availability at which $I$ reaches half of its maximum	$\text{g m}^{-2}$	100	Owen-Smith (2002)
$q$	Coefficient of the decrease in grass quality with increasing standing biomass	–	0.0019	Prins and Olff (1998)
$bh_{max}$	Maximum reachable height of the browsers	m	5	
$adj$	Proportion of $\lambda$ that is removed from adjacent cells	–	0.1	
$wf$	Exponent for the weighting of a cell	–	–3	

large proportion of the world's human population and a majority of its rangeland and livestock (Scholes and Archer 1997), understanding the role of herbivores in vegetation patterning in these ecosystems is urgently required (Sankaran et al. 2005), moreover because savannas are among the ecosystems that are most sensitive to future changes in land use and climate (Sala et al. 2000, Bond et al. 2003, House et al. 2003).

In this paper, we therefore focus on the mechanisms through which herbivores induce or modify spatial patterning in savanna vegetation. We do this by modelling herbivore–vegetation interactions in a spatial context and analysing the key assumptions that are required for herbivores to induce spatial patterning. We focus on two basic mechanisms of plant–herbivore interactions that we consider important for vegetation patterning to occur: self-facilitation and spatial dependency of foraging. Self-facilitation is the process where herbivores increase the attractiveness of a site while foraging. This process occurs when herbivory enhances the quality or quantity of regrowth following defoliation. The former has often been observed when nutrient concentration is increased in post-defoliation regrowth through the replacement of older, low-quality leaves by younger, high-quality tissue (Anderson et al. 2007). The latter applies when herbivory leads to an increased amount of regrowth following defoliation or adjustment of the vertical stratification of forage material, thereby influencing the availability of reachable forage (Fornara and Du Toit 2007). Spatial dependency of foraging is the process where the interaction of herbivory

with vegetation at a site is influenced by the surroundings of the site. For example, vegetation characteristics at larger spatial scales can influence the selection of sites to forage (Senft et al. 1987). Accordingly, the surrounding matrix of a site can be positive (attractive) or negative (repellent) in the herbivore's choice of a particular site (Baraza et al. 2006). Moreover, herbivores do not only forage strictly in selected sites, but also in the close surroundings of that site (Cid and Brizuela 1998, Adler et al. 2001, Baraza et al. 2006).

We include these processes in our modelling exercise because they are mentioned in many studies on herbivore foraging in relation to pattern formation (Prins and Van der Jeugd 1993, Cid and Brizuela 1998, Adler et al. 2001, Woolnough and Du Toit 2001, Baraza et al. 2006, Fornara and Du Toit 2007). By analysing the conditionality of these processes for vegetation pattern formation to occur, we try to increase our understanding of the mechanisms through which herbivores induce spatial patterning in savanna vegetation. Additionally, we analyse the effects of herbivore density and the initial landscape configuration on the role of herbivores in vegetation patterning. Focusing only at the influence of herbivory while leaving out other determinants like fire, nutrient cycling or water redistribution and their possible interactions allows us to isolate the effect herbivores can have on vegetation patterning. Hence, we aim at contributing to a better understanding of the role of herbivory as a determinant of spatial vegetation patterning in savanna ecosystems.

## The model

### Model overview

We developed a spatially explicit, cell-based model that simulates vegetation dynamics in each cell based on availability of and competition for resources between grasses and trees. We then introduce herbivores into the simulated landscape, both grazers, foraging only on grass, and browsers, foraging exclusively on trees. The spatial pattern of biomass removal through herbivory is modelled to be determined by the spatial distribution of the herbivores. Through varying parameter values, we analyse the influence of herbivory on vegetation patterning. Our simulations are run in a landscape covering a lattice with  $200 \times 200$  cells of  $5 \times 5$  m each. To avoid edge effects, the simulated landscape is torus-shaped. The maximum time span of each simulation run is 1000 annual time steps, but the simulation is finished when the state variables remain constant for 50 years. The processes, variables and parameters (Table 1) involved are discussed below, in order of appearance of the three main components in the flow of the model: resource availability, vegetation dynamics and herbivory. We then outline the methods of model analyses and scenarios that are simulated.

### Resource availability

Following the majority of models that study savanna tree-grass dynamics (Walter 1971, Walker et al. 1981, Walker and Noy-Meir 1982, Eagleson and Segara 1985, Higgins et al. 2000, Van Wijk and Rodriguez-Iturbe 2002, Fernandez-Illescas and Rodriguez-Iturbe 2003, Van Langevelde et al. 2003), we consider available moisture as the main resource limiting plant growth and neglect competition for nutrients. We used the two-layer hypothesis (Walter 1971) as the basis for water distribution in the soil and availability for tree and grass growth. This hypothesis assumes niche separation in the rooting zone of grasses and trees. Grasses are the superior competitors for moisture in the topsoil layer (i.e. grass root zone), where both grasses and trees have roots. In the subsoil layer (i.e. tree root zone), the competitive ability of trees is dominant, since only a negligible proportion of the grass roots penetrate to this depth (Weltzin and McPherson 1997, Schenk and Jackson 2002). Following Van Langevelde et al. (2003), we assume that all water that infiltrates in the soil on a yearly basis is available for the growth of grasses and trees. This infiltrated water first increases the soil moisture content in the grass root zone. Above a certain threshold, water starts to percolate from the grass root zone into the tree root zone. We assume that both rooting zones are not water saturated in savannas. The recharge rate of moisture in the grass root zone ( $w_t$ ) can then be given by:

$$w_t = w_{in} - w_s \quad (1)$$

where  $w_{in}$  is the amount of infiltrated water per year and  $w_s$  is the rate of moisture recharge in the tree root zone (Van Langevelde et al. 2003). The parameter  $w_s$  is proportional to the amount of infiltrated water:

$$w_s = \alpha(w_{in} - \beta) \quad \text{if } w_{in} > \beta \quad \text{else } w_s = 0 \quad (2)$$

where  $\beta$  is the soil moisture content in the grass root zone above which water starts to percolate to the tree root zone, and  $\alpha$  is the proportion of excess water above  $\beta$  that percolates to the tree root zone.

### Vegetation dynamics

The model features the vegetation components grass biomass ( $H$ , consisting of grasses and herbs) and woody biomass ( $W$ , consisting of wood, twigs and leaves of trees and shrubs). The rate of change of aboveground grass biomass over one year can be calculated as follows (Walker et al. 1981, Walker and Noy-Meir 1982, Van Langevelde et al. 2003):

$$\frac{dH}{dt} = r_H w_t \frac{H\theta_H}{H\theta_H + W\theta_W + w_s} - d_H H - L_{HH} \quad (3)$$

where  $r_H$  is the water use efficiency of grass,  $\theta_H$  and  $\theta_W$  the rates of water uptake per unit biomass of grasses and trees, respectively,  $d_H$  the specific loss of grass biomass due to mortality and senescence, and  $L_{HH}$  the loss of herbaceous biomass due to grazing. The rate of change of woody biomass over one year can be represented by:

$$\frac{dW}{dt} = r_W w_t \left( \frac{W\theta_W}{H\theta_H + W\theta_W + w_s} + w_s \right) - d_W W - L_{WH} \quad (4)$$

where  $r_W$  is the water use efficiency of trees,  $d_W$  the specific loss of woody biomass due to mortality and senescence, and  $L_{WH}$  the loss of woody biomass due to browsing (Van Langevelde et al. 2003). Without herbivores, grasses are able to dominate when the amount of infiltrated water is below  $\beta$  (Walker and Noy-Meir 1982). Trees and grasses co-occur when the amount of infiltrated moisture is above this threshold and below the availability at which trees start dominating the vegetation. With increasing moisture availability, the vegetation thus shows transitions from grassland to savanna to woodland (Walker and Noy-Meir 1982, Van Langevelde et al. 2003).

Since the vertical structure of woody biomass determines the herbivores' access to browse, we expanded the two-dimensional vegetation model as described above with the vertical dimension. For simplicity, our model does not track individual trees, but rather height cohorts of identical individuals. Twenty cohorts (that can co-occur in a single cell) represent the vertical structure of the woody vegetation. A cohort is defined here as a group of individual trees with the same height and other characteristics (e.g. size and shape, all being an allometric function of tree height). The shortest cohort contains trees of 0.5 m in height and subsequent cohorts increase in height with 0.5 m increments up to the tallest cohort of 10 m tall trees. Trees of each cohort are characterised by their height ( $h_t$ ), canopy bottom height ( $h_b$ ), canopy midpoint height ( $h_m$ ), canopy width ( $c_w$ ), total aboveground biomass and a browseable/non-browseable biomass allocation ratio, where large trees have proportionally less browseable biomass than small trees. Browseable biomass is the part of the plant that is eaten by browsers and consists mainly of leaves, but could contain a small proportion of branches. To provide an

idealised canopy geometry that closely mimics the shape of a typical savanna tree crown (Caylor and Shugart 2004), canopy width at each layer  $d$  in the canopy ( $c_{w,d}$  with  $h_b < d < h_t$ ) is modelled as:

$$c_{w,d} = \sqrt{c_w^2 \left(1 - \frac{(d - h_m)^2}{(h_t - h_m)^2}\right)} \quad \text{if } d - h_m \geq 0 \quad (5)$$

$$c_{w,d} = c_w \exp\left(4 \frac{d - h_m}{h_m}\right) \quad \text{if } d - h_m < 0$$

With the total biomass of each cohort in a cell, the browseable biomass is calculated for each cohort and the vertical zonation of all browse in a cell is calculated for height layers with 0.5 m increments. Multiple cohorts can thus contribute browseable biomass to a single height layer.

Due to growth, trees in a cohort can shift to the next cohort. This increases the total biomass of that cohort, and thus the total woody biomass in the cell. Due to mortality, woody biomass is removed from a cohort, thereby decreasing the total woody biomass in the cell. These two processes, i.e. growth and mortality, are operating simultaneously in each cell, resulting in a change of biomass as calculated with Eq. 4. The change in biomass is allocated to the different cohorts as a function of the amount of intercepted light per cohort. Growth is modelled to be positively related to the amount of intercepted light per cohort, while for mortality and senescence the relation is negative. Thus, cohorts that intercept a lot of light largely contribute to the increase of woody biomass and experience only small losses. The light intensity at each layer  $d$  in the canopy ( $I_d$ ) is calculated using the Lambert-Beer equation:

$$I_d = I_{in} e^{-kW_{b,d}^+} \quad (6)$$

where  $I_{in}$  is the incident light intensity above the canopy,  $k$  is the light extinction coefficient and  $W_{b,d}^+$  is the total amount of biomass above layer  $d$  (Huisman et al. 1997). The amount of intercepted light of cohort  $c$  ( $Int_c$ ) is subsequently calculated as:

$$Int_c = \sum_{d=0}^{h_t} [I_{in} e^{-kW_{b,d}^+} (1 - e^{-kW_{b,c,d}})] \quad (7)$$

where  $W_{b,c,d}$  is the amount of biomass of cohort  $c$  at layer  $d$ . Trees in the highest cohort do not grow since they are assumed to have reached their maximum size. Likewise, biomass gain due to regeneration is kept at a constant proportion of the change in woody biomass as calculated with Eq. 4. Consequently, without disturbance such as browsing, the woody biomass in a cell grows to the equilibrium standing biomass, consisting exclusively trees in the highest cohort (Fig. 1).

## Herbivory

The browser and grazer populations are simulated as herds that can move freely in the landscape and have complete knowledge regarding the distribution of their food resources. Using an ideal free distribution approach (Fretwell and Lucas 1970), herbivores select cells to forage based on the attractiveness of cells. If several cells have the same attractiveness, the herbivores choose one of the cells at random. Within the yearly simulation loop for plant

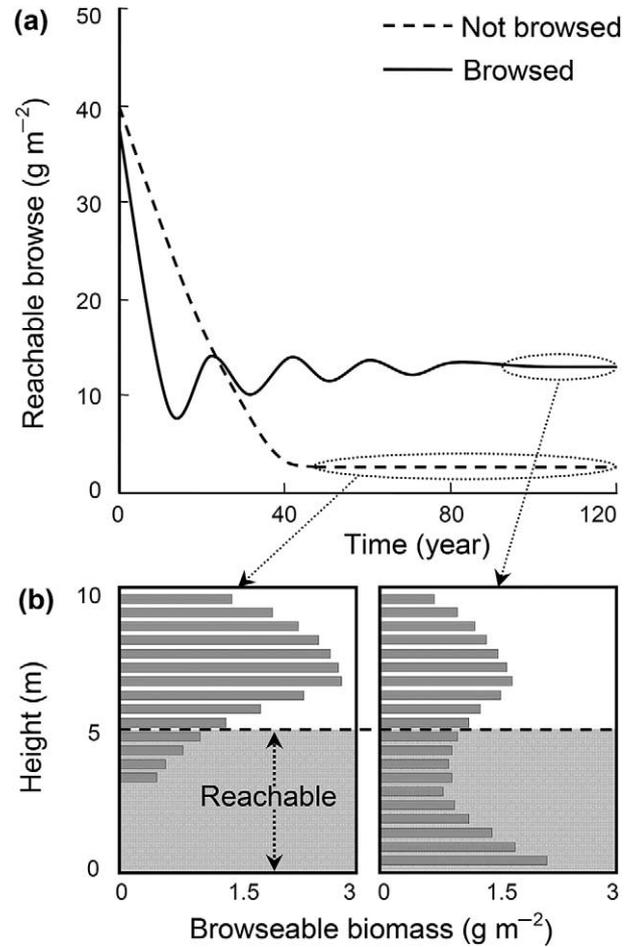


Fig. 1. (a) Dynamics of reachable browseable biomass (i.e. browse between 0–5 m high) in a cell for a scenario without (dashed line) and with browsing (continuous line) for an initial situation where all cohorts have an equal amount of biomass. (b) Vertical stratification of browseable biomass with and without browsing after the system stabilised. Although browsing removes biomass in the short term, it stimulates regrowth and regeneration and thereby enhances the amount of reachable browse by keeping the trees short.

growth, a foraging loop is implemented. In each step of the foraging loop, the attractiveness of all cells is calculated, and the cell with the highest attractiveness is selected. The herbivores remove  $\lambda$  gram of biomass from the selected cell, and then the next foraging step follows. The foraging loop continues until the requirements of the herbivore population are met and the total amount of forage consumed in a cell determines  $L_{HH}$  (Eq. 3) and  $L_{WH}$  (Eq. 4) for each cell in the simulated landscape.

In the analysis of the effect of herbivory on vegetation patterning, the population sizes were kept constant. Although it is obvious that a constant population size does not hold in large natural systems, we used this assumption because (1) the study was performed in a relatively small area and, more importantly, (2) because we want to isolate the effect of herbivory on vegetation patterning and do not want to include interactive effects of herbivore dynamics. The yearly population food requirement ( $req_p$ ) is calculated as:

$$\text{req}_p = f_d p_{\text{size}} \quad (8)$$

where  $f_d$  is the yearly food intake as proportion of the body mass of the foragers and  $p_{\text{size}}$  is the population size in total biomass (Owen-Smith 2002).

The effect of the herbivores on landscape heterogeneity depends on the interaction between the pre-existing spatial pattern of the vegetation and the spatial pattern of herbivory (Bakker et al. 1984, Adler et al. 2001), which is determined by the distribution of the herbivores. Herbivore distribution itself is determined by various factors (Coughenour 1991, Bailey et al. 1996, Hobbs 1996, 1999, Adler et al. 2001), but in our model, we confine ourselves to forage as one of the prime determinants. Both forage availability and forage quality play an important role in herbivore distribution: selective foraging occurs in preferred areas. According to optimal foraging theory, animals forage in a way that maximises the immediate rate of energy gain (Stephens and Krebs 1986). Therefore, the instantaneous energy gain through consuming resources in a cell is taken as measure for the attractiveness of a cell for herbivores. This attractiveness does not only depend on the instantaneous intake rate of food, but also on the digestible energy content of the food (Prins and Olff 1998, Owen-Smith 2002, Drescher et al. 2006). We calculate the instantaneous intake rate (I) for both grazers and browsers by means of an asymptotic type II functional response:

$$I = \frac{i_{\text{max}} F}{g_{1/2} + F} \quad (9)$$

where  $i_{\text{max}}$  is the maximum food intake rate at high food abundance,  $F$  is the food availability and  $g_{1/2}$  is the food availability at which  $I$  reaches half of its maximum (Owen-Smith 2002). Only the amount of browseable woody biomass within the physical reach of the browsers is considered as available browse, while the total amount of herbaceous biomass is assumed available for the grazers. The instantaneous rate of energy gain from consuming forage in a cell ( $E$ ) can be calculated by adding a reduction term for the digestibility of the forage material (Owen-Smith 2002):

$$E = \frac{i_{\text{max}} F}{g_{1/2} + F} (1 - q)^F \quad (10)$$

where  $q$  is the reduction term of forage digestibility with increasing standing biomass. Digestibility of grass biomass has been reported to be negatively correlated with standing biomass (Prins and Olff 1998, Anderson et al. 2007), while the digestibility of browseable material remains constant (Woolnough and Du Toit 2001).

### Self-facilitation

In our model, the herbivores interact with the vegetation by influencing the vegetation characteristics while foraging (standing biomass, forage quality or vertical zonation), which, in turn, determine the attractiveness of a cell to the herbivores. The mechanism for self-facilitation through grazing is the decreasing nutritive quality of grass vegetation with increasing standing biomass as in Eq. 10. Hence, grazers increase the attractiveness of grazed cells by

decreasing the standing crop and simultaneously increasing the nutritive quality of vegetation. Grazed cells are consequently visited repeatedly as long as regrowth of the grass is faster than the time within which grazers return. In contrast to grazers, browsers do not experience a decline in forage quality with increasing standing woody biomass. Browsers select cells with the highest amount of browseable biomass that is within their reach because of the vertical structure of the woody vegetation. Although browsing results in a decrease of the amount of reachable forage in the short term, the amount of accessible browse in the long term remains high relative to a situation without browsers (Fig. 1). Hence, browsers are able to facilitate themselves by increasing the amount of available (i.e. reachable) forage by keeping the trees short and stimulating the regeneration and regrowth of woody vegetation. These above-mentioned results show that the herbivores exhibit self-facilitation, either by increasing the nutritional quality of regrowth following defoliation, or by inducing changes in resource allocation and plant architecture (i.e. vertical zonation of browseable biomass). Hence, foraging in a cell increases the attractiveness of the cell and thereby the chance that the cell will be selected in the near future.

### Spatial dependency of foraging

The distribution of the herbivores does not only depend on the attractiveness of single cells, it may also result from decisions made by the animals at larger spatial scales (Senft et al. 1987, Bailey et al. 1996). Herbivores are thought to select the landscape unit richest in resources, then the most productive locations within this landscape unit, and so on, down to the most palatable species within a feeding station (Bailey et al. 1996). Foraging decisions at broad spatial scales thus can constrain choices at smaller scales (Bailey et al. 1996). We therefore calculate the attractiveness of a cell as a weighted average of the attractiveness of all cells in its vicinity using inverse distance weighting:

$$w = \text{dist}^{-wf} \quad (11)$$

where  $w$  is the weighting factor of a cell and  $wf$  is the weighting exponent of a cell with distance  $\text{dist}$  to the cell of focus. In this way, the attractiveness of large-scale landscape units influences the attractiveness of a single cell within this unit.

Herbivory at a certain location also affects the vegetation in neighbouring locations, as the proximity of palatable plants can increase the herbivore damage to both palatable and unpalatable plants in the surroundings (Baraza et al. 2006). While foraging in a cell, the herbivores are therefore modelled to also remove a constant fraction ( $\text{adj}$ ) of  $\lambda$  from the adjacent cells.

### Model analyses

Following Murwira and Skidmore (2005), we used variograms to quantify the spatial heterogeneity of the simulated landscapes by quantifying the heterogeneity and dominant scale of these landscapes, where dominant scale is a measure for the average vegetation patch size. A variogram expresses the degree of spatial variation of a regionalised variable, here

grass and woody biomass, as a function of distance:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_{i+h})]^2 \quad (12)$$

where  $\gamma(h)$  is the semivariance at lag  $h$  (i.e. the beeline distance between sample locations  $x_i$  and  $x_{i+h}$ ),  $N(h)$  is the number of observation pairs separated by  $h$ ,  $z(x_i)$  is the value of the regionalised variable at location  $x_i$ , and  $z(x_{i+h})$  is the value of the regionalised variable at distance  $h$  from  $x_i$  (Murwira and Skidmore 2005). To calculate the empirical variograms and to fit an exponential variogram model through the data (Fig. 2), we used the statistical package R (ver. 2.5.1, R Development Core Team) with the Gstat library for geo-statistical analyses (Pebesma 2004, 2007). The two main structural parameters of the variogram, the sill and the range (Fig. 2) are calculated and used to measure respectively the heterogeneity and dominant scale of vegetation.

### Simulations

We simulated model scenarios with variation in parameter values and initial landscapes. We started with simulations where both self-facilitation and spatially explicit foraging were systematically included in the model to understand their independent effects on spatial pattern formation as well as their interactive effects. We then performed simulations in which we varied the densities of the browsers and grazers. All of these simulations were performed on initial landscapes that had random amounts of grass and tree biomass in each cell drawn from a uniform distribution.

Finally, we performed a series of simulations in which we incorporated both different levels of heterogeneity as well as different dominant scales of the initial landscape. Different levels of heterogeneity in the initial landscapes were obtained by changing the minimum and maximum values

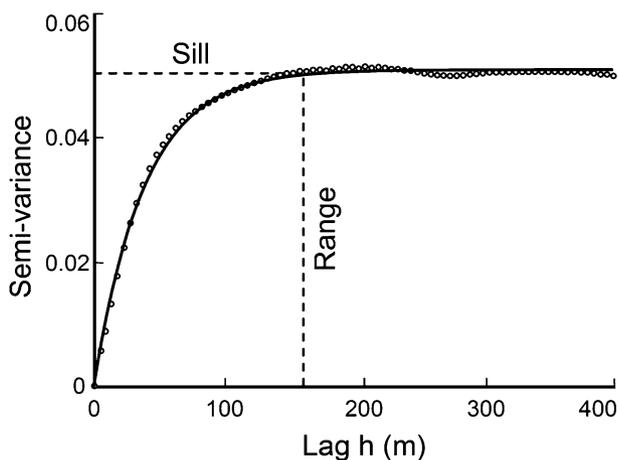


Fig. 2. The use of variograms to express the degree of spatial variation of grass and woody biomass as a function of lag distance  $h$ . The sill of the variogram (i.e. the semi-variance where the variogram levels off) is used to measure the heterogeneity of the simulated landscapes, while the range (i.e. the lag-distance where the variogram levels off) is used as a measure for the dominant scale of the vegetation patterns.

between which random values for grass and woody biomass were drawn. Different dominant scales of the initial landscapes was introduced by grouping cells together and assigning them the same random value for grass or woody biomass.

### Results

If we analyse the model without herbivores, the resultant standing biomass of trees and grasses in each grid cell is only determined by the amount of infiltrated water and the soil characteristics, with dynamics as outlined by Van Langevelde et al. (2003). Since we kept the amount of infiltrated water and soil characteristics equal for all cells and constant during the simulations, every cell is identical to the others resulting in homogeneous vegetation without patterning, regardless of the initial landscape conditions. The tree layer then consists exclusively of trees in the highest cohorts, for there are no disturbances that prevent the trees from growing tall (Fig. 1).

### Conditions for herbivores to induce vegetation patterning

If we exclude both self-facilitation and spatial dependency of foraging from the model (i.e. grazing does not increase the nutritional quality of grass vegetation, the browsers can access the entire tree canopy, and the selection of a cell is not influenced by its neighbourhood), the herbivores create a landscape with only fine-scale cell-to-cell variation, but

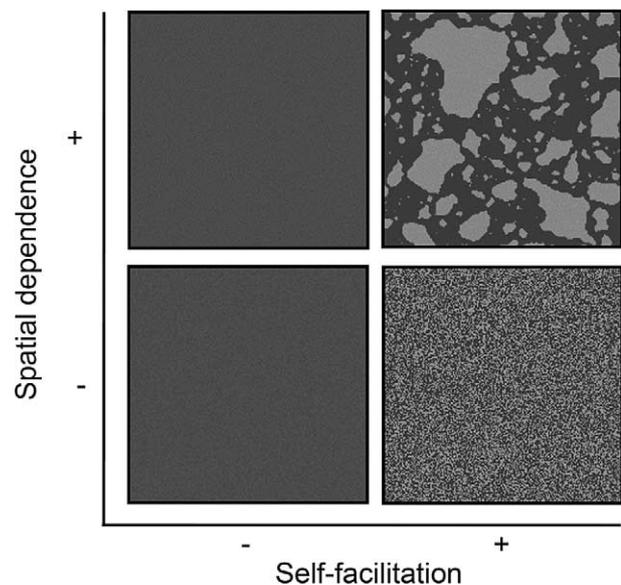


Fig. 3. Vegetation patterns after 500 year of simulation in relation to the two driving mechanisms: spatial dependency of foraging and self-facilitation, where  $-$  means that the assumption is not included in the model, whereas  $+$  means that the assumption is included in the model. Both assumptions need to be simultaneously included in order to induce vegetation patterning. The grey tone represents the amount of biomass, with dark grey expressing a high biomass, and light grey a low biomass. The landscapes confine  $200 \times 200$  cells of  $5 \times 5$  m each.

without broad-scale vegetation patterns (Fig. 3). The fine-scale heterogeneity in vegetation results from a reduction of forage material in the cells where the herbivores fed relative to the surrounding matrix. In this scenario, the herbivores select only the cells with the highest standing biomass, irrespective of the cell's location. Foraging decreases the attractiveness of these cells and thus the chance that they are selected in the near future. When including self-facilitation, but excluding spatial dependency of foraging, the resultant landscape shows only fine-scale patterning due to selective foraging in preferred cells (Fig. 3). Due to self-facilitation, selected cells are frequently revisited, but the selection of sites is not influenced by the spatial arrangement of the sites. When spatial dependency of foraging is included, but self-facilitation excluded from the model, there is no reason for the herbivores to frequently revisit a site and hence they create virtually homogeneous vegetation with only slight cell-to-cell heterogeneity (Fig. 3). Only when both key assumptions are simultaneously included, the herbivores are able to create stable, broad-scale vegetation patterns (Fig. 3).

The herbivores then frequently revisit sites due to self-facilitation, where larger patches are preferred above smaller ones due to spatial dependence of foraging.

To understand the separate effects of the components of self-facilitation and spatial dependency of foraging on vegetation patterning, we analyse the model, varying the parameters  $wf$ ,  $adj$ ,  $q$  and  $bhmax$ , while calculating the dominant scale and heterogeneity of the resultant landscapes. An increase of the weighting of surrounding cells in the assessment of a cell's attractiveness ( $wf$ ) or the amount of forage consumed in adjacent cells ( $adj$ ) results in an increase of the dominant scale of the vegetation patterns, but the heterogeneity remains relatively unaffected (Fig. 4a–b). Increasing the decrease of forage quality with increasing grass biomass ( $q$ ) increases the heterogeneity and dominant scale of the resultant vegetation (Fig. 4c). This means that when grazers are more able to increase the forage quality while foraging, the grazed patches become larger, and the spatial heterogeneity becomes higher. The dominant scale of the vegetation increases with increasing  $q$  since grazing

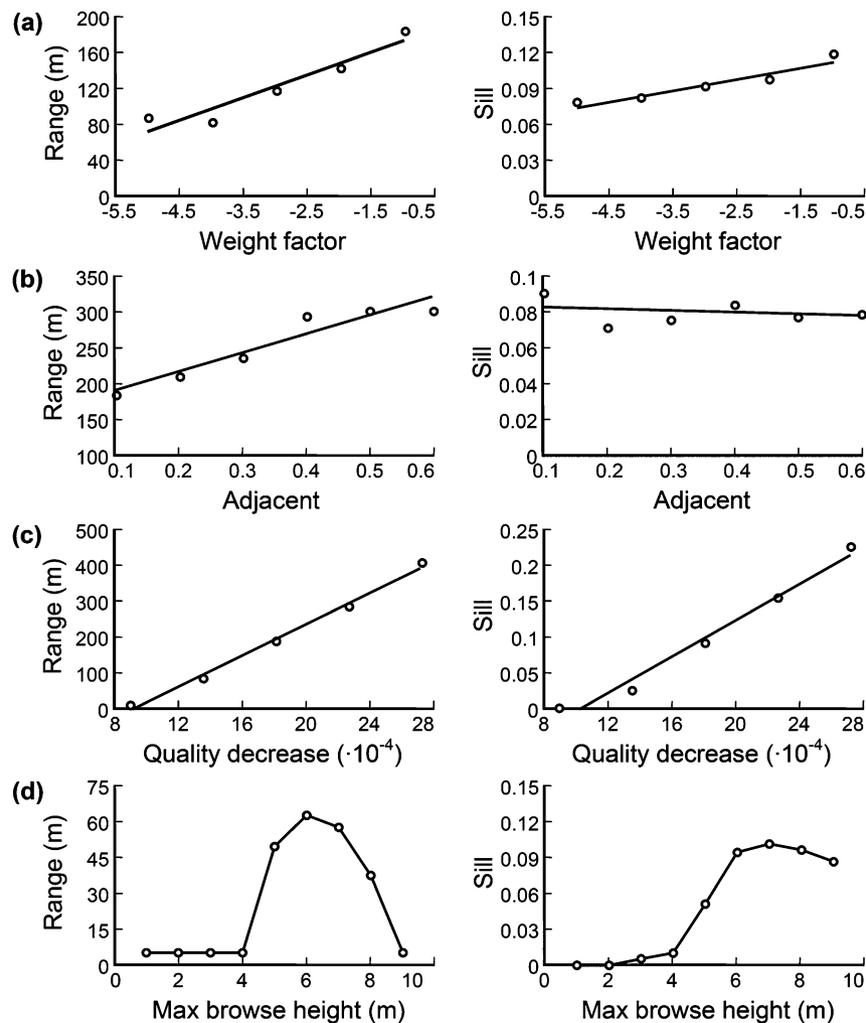


Fig. 4. The range and sill of the variograms as measure for the dominant scale and heterogeneity of the vegetation patterns (Fig. 2) while varying parameter settings for spatial dependency of foraging: (a) the weighting exponent of neighbouring cells ( $wf$ ) and (b) the fraction of  $\lambda$  that is removed from adjacent cells ( $adj$ ), and self-facilitation: (c) the decrease of nutritional quality with increasing grass biomass ( $q$ ) and (d) the height till which the browsers can reach ( $bhmax$ ). All parameter values as in Table 1 except for the parameter under change.

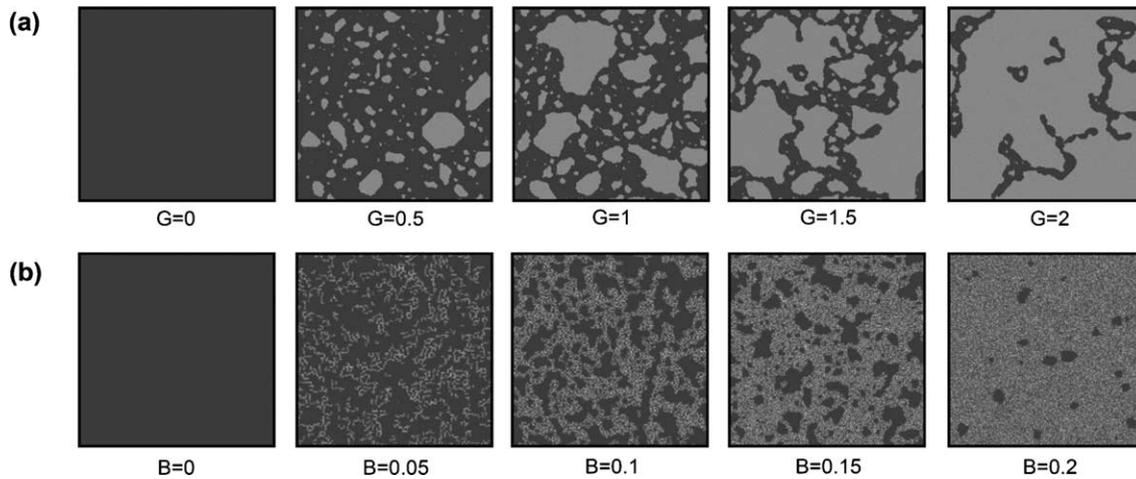


Fig. 5. Stable patterns in grass (a) and woody (b) vegetation after 500 yr of simulation as a function of grazer (G) and browser (B) density ( $\text{g m}^{-2}$ ), respectively. The grey tones represent the amount of grass or woody biomass, with dark grey expressing a high biomass, and light grey a low biomass. Each landscape confines  $200 \times 200$  cells of  $5 \times 5$  m each.

increasingly facilitates the quality of forage material, also in adjacent cells, and this in turn increases the attractiveness of the selected cell, but also the attractiveness of the cells in its near surroundings. Through altering the maximum height that the browsers can reach (bhmax), we see that the browsers only induce spatial vegetation patterning when they are able to access a large part of the tree canopy, but not entirely (Fig. 4d). Only then are browsers able to facilitate themselves, for they are able to suppress the woody vegetation, in which case there would be more reachable forage compared to an unbrowsed situation (Fig. 1). When the browsers can only access a small proportion of the tree canopy, their ability to suppress the woody vegetation is limited, and hence self-facilitation is not important for them. When the browsers can access the entire tree canopy, there is no self-facilitation and hence no vegetation patterning, for it is not necessary to alter the plant

architecture in order to increase the amount of reachable browse.

### Changing herbivore density

In the previous section, we showed that both key assumptions have to be included simultaneously in the model to induce spatial vegetation patterning. We now analyse the behaviour of the model while including both mechanisms simultaneously and varying herbivore densities. At low grazing pressure, the grazers create small grazed patches (Fig. 5a). With increasing grazing pressure, the grazed patches become larger, until eventually the grazers exploit the entire landscape and create only fine-scale cell-to-cell heterogeneity, as explained above. As a result, the heterogeneity and dominant scale of the vegetation show a hump-shaped response to increasing grazing pressure (Fig. 6a).

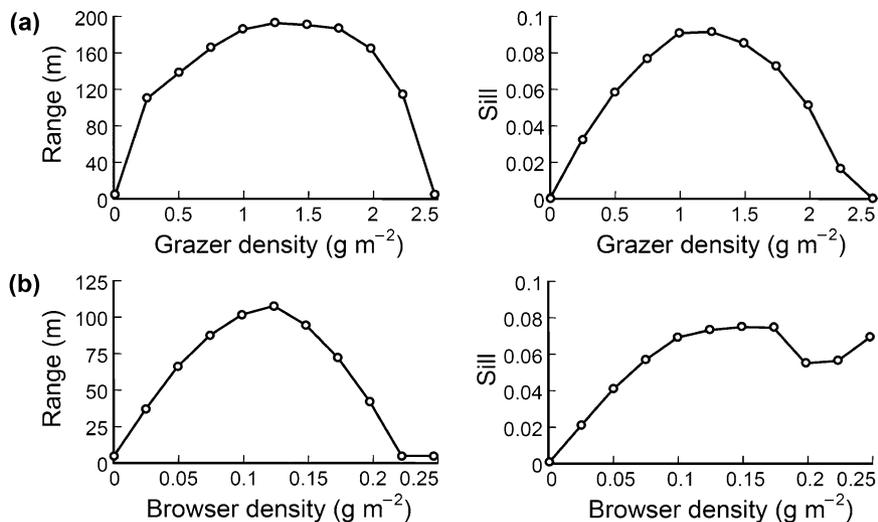


Fig. 6. The dominant scale (i.e. range, Fig. 2) and heterogeneity (i.e. sill) of the vegetation in relation to (a) grazer density and (b) browser density.

The same holds for the browsers: at low browser density, the browsers suppress the woody vegetation in the cells that they select to forage, while the trees in unutilised cells are able to grow to full size, resulting in browsed patches of small trees surrounded by large trees. With increasing browser density, the browsed patches grow in size until the browsers utilise almost the entire woody vegetation, with only scattered areas of unbrowsed vegetation (Fig. 5b). When browser density then increases even more, they are able to suppress the entire woody vegetation, creating spatially homogeneous vegetation at a broad scale, with only fine-scale differences in biomass removal from selected and adjacent cells. The dominant scale and heterogeneity of the woody vegetation therefore also show a hump-shaped response to browser density (Fig. 6b).

### Interactions with pre-existing vegetation patterns

Analysis of the model with different initial landscape configurations shows that both the heterogeneity of the initial vegetation as well as the dominant scale of the pre-existing vegetation patterns influence the vegetation patterns as produced by the herbivores (Fig. 7). The dominant scale of the resultant vegetation patterns increases when the dominant scale of the initial vegetation increases (Fig. 7a), meaning that the level of adherence of the herbivores to forage in pre-existing patches increases when these pre-existing patches increase in size. With increasing heterogeneity of the initial landscape, the dominant scale of the resultant vegetation decreases (Fig. 7b).

### Discussion

In this paper, we address the question whether and through which mechanisms herbivores can induce spatial patterning in savanna vegetation, and how the role of herbivory as a determinant of vegetation patterning changes with variation in herbivore density and the pre-existing pattern of

vegetation. To answer these questions, we developed a spatially explicit simulation model, including growth of grasses and trees, vertical zonation of browseable biomass, and spatially explicit foraging by grazers and browsers. The trends produced by the model show that the formation of spatial vegetation patterns in savannas due to herbivory critically depends on the interaction between two mechanisms, namely self-facilitation by the herbivores and spatial dependency of foraging. This means that (1) there has to be a reason for herbivores to revisit a site, e.g. through an increased availability or quality of forage, and (2) foraging at a site should relate to vegetation at larger spatial scales.

Self-facilitation can emerge from increasing the nutritional quality of vegetation or increasing the forage availability while foraging. In our model, the first case applies to the grazers, while the latter one is applicable to the browsers. Adler et al. (2001) argue that feedbacks between grazing and plant quality may be important sources of spatial patterning since they promote the continued use of previously grazed patches. These feedbacks include increased nutritional content of the forage material, a reduction in senescent material and maintenance of leaves in an early phenological state (Coppock et al. 1983, McNaughton 1984, Jefferies et al. 1994, Hobbs 1999, Anderson et al. 2007). The vegetation patterns of grass biomass as produced by our model resemble the “grazing lawn” phenomenon where ungulate grazers are able to maintain permanent grazing lawns through a positive feedback loop (grazing–regrowth–regrazing) that generates enhanced productivity in a short sward (McNaughton 1984, Anderson et al. 2007). The model output also resembles the vegetation patterns that Bakker et al. (1984) and Cid and Brizuela (1998) found as result of grazing by sheep and Aberdeen Angus steer, respectively, on initially uniform paddocks. They showed that the sheep and cattle revisited some sites within the paddocks more often while neglecting other sites, resulting in a mosaic of heavily utilised and lightly utilised patches, as do our simulated grazers.

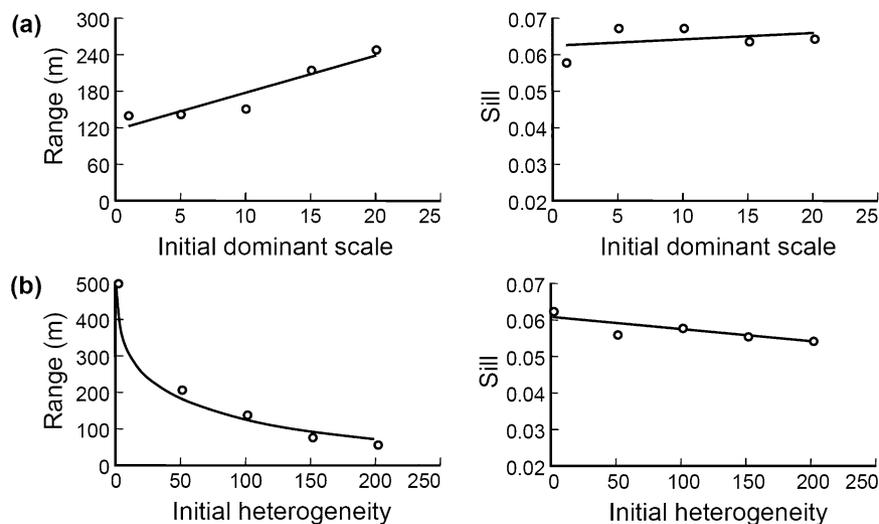


Fig. 7. The dominant scale (i.e. range, Fig. 2) and heterogeneity (i.e. sill) of the simulated vegetation in relation to (a) the dominant scale of the initial landscape ( $d_s$ , where  $d_s$  by  $d_s$  cells are all assigned the same random value of grass biomass), and (b) the heterogeneity of the initial landscape ( $i$ : computed as the interval  $280 \pm i$  out of which random values are drawn to be assigned to each cell).

While grazing enhances the quality of forage material in our model, browsing increases the amount of browse within reach of the herbivores. High browsing pressure can prevent the establishment of woody seedlings and retard the growth of shrubs, suppressing their recruitment into the mature stage (Pellew 1983, Prins and Van der Jeugd 1993, Roques et al. 2001, Augustine and McNaughton 2004, Fornara and Du Toit 2007). In this way, patches are created where trees are being suppressed by the browsers while in other areas trees can escape this suppression and reach a “size refuge” when the browsers are not able to suppress the entire woody vegetation (Fornara and Du Toit 2007). Analogous to the grazing lawns, Fornara and Du Toit (2007) call these browsed patches “browsing lawns” since chronic browsing by ungulates can maintain trees in a suppressed and hedged state, thereby inducing changes in resource allocation and plant architecture and hence making more food available to browsers.

Although self-facilitation is a prerequisite for vegetation patterning to occur in our model, we claim that self-facilitation alone is not sufficient to induce spatial patterning in savanna vegetation through herbivory. The interaction of self-facilitation with spatial dependency of foraging is found to be crucial to induce patterning. We modelled spatial dependency of foraging by including the attractiveness of a cell's environment in the assessment of the attractiveness of the particular cell, and by foraging in cells adjacent to selected cells. The first case can be interpreted as hierarchical foraging decisions (Senft et al. 1987, Bailey et al. 1996), where herbivores make decisions at different spatial-temporal scales and where large-scale decisions influence decisions at smaller scales. The herbivore pressure at a certain location also results in consuming the vegetation at neighbouring locations, as the proximity of palatable plants can increase the herbivore damage to both palatable and unpalatable plants in the surroundings (Baraza et al. 2006). This effect of foraging at neighbouring locations is small when the central location attracts few herbivores, and it decreases with increasing distance from the central location to which the herbivores are attracted.

Analysis of our model shows that the heterogeneity and dominant scale of the resultant vegetation patterns is highest at intermediate herbivore densities. With higher herbivore densities, the herbivores are forced to be less selective, and hence the level of heterogeneity of the vegetation decreases. These findings are consistent with the predictions from Adler et al. (2001) that the heterogeneity of vegetation decreases when the removal of plant tissue through herbivory is distributed spatially more homogeneous. Our model also shows that the pre-existing pattern of vegetation increasingly influences vegetation patterning through herbivory when the heterogeneity of the initial landscape increases. Adler et al. (2001) postulate that when grazing is a dependent function of the pre-existing vegetation pattern (termed “selective grazing” in their paper), then patterns emerge only if grazing positively influences the resource levels of grazed patches (i.e. self-facilitation), and otherwise patterns will disappear. We also generated this hypothesis because only through the inclusion of self-facilitation spatial vegetation patterns could be produced. Additionally, we showed that the influence of the pre-existing vegetation in determining vegetation patterning

through herbivory decreases when the initial heterogeneity and dominant scale of the initial vegetation is smaller. With initially low vegetation heterogeneity, the herbivores are able to shape the vegetation, but they adhere more to the pre-existing vegetation patterns when the initial vegetation heterogeneity increases. Although the heterogeneity and dominant scale of the initial landscapes do influence the dominant scale of the resultant landscapes, they do not severely influence the heterogeneity of the resultant landscapes, suggesting the heterogeneity of the resultant landscapes is more a property of the herbivores than it is influenced by the initial landscape configuration.

Contrary to our finding that self-facilitation is a necessary mechanism to induce spatial patterning in savanna vegetation, the positive effect of repeated grazing on forage quality can decline in the long term, when grazing remains intensive and leads to a change in plant species composition to less palatable species (Coppock et al. 1983). As we did not take plant species composition into account, our model could not reproduce this reversing effect. Furthermore, overgrazing can lead to an increase of woody vegetation at the cost of palatable grasses, often referred to as “bush encroachment” (Roques et al. 2001). In our model, the simulated grazers and browsers forage exclusively on grass and woody vegetation, respectively. Hence, the grazers do not directly influence the woody vegetation, but only indirectly through removing grass biomass in selected cells, thereby decreasing the competitive ability of the grass vegetation and stimulating the growth of trees. Likewise, the browsers do not directly influence the grass vegetation, but only indirectly through influencing resource competition between grasses and trees. Hence, grazing at a site increases the competitive advantage of trees and therefore the biomass of the woody vegetation, what corresponds to the bush encroachment phenomenon that is often observed. However, the increased growth of woody vegetation attracts more browsers which, when the browser density is high enough, can suppress the woody vegetation as shown above. This might diminish the risk of bush encroachment. Because we did not model individual species but only plant functional groups, the negative effect of an increased biomass of the woody vegetation on grass species composition and palatability could not be reproduced. Nevertheless, the reversing effects of herbivory on forage characteristics could reduce or contradict the mechanism of self-facilitation that we postulate above.

Recently, a body of theory has emerged emphasizing a scale-dependent feedback between localized facilitation and large-scale inhibition of plant growth driving patterning and self-organisation in vegetation (Klausmeier 1999, Rietkerk et al. 2002, 2004, Kéfi et al. 2007, Scanlon et al. 2007, Van Wesenbeeck et al. 2008). In arid systems, for example, infiltration of water is locally enhanced by plant presence, while on landscape scales competition for water between plants is the dominant process explaining observed vegetation patterns (Rietkerk et al. 2002, Van Wesenbeeck et al. 2008). In this paper, we posit an alternative mechanism behind spatial patterning in savanna vegetation, namely the interaction between spatial dependent selectivity of herbivores and forage enhancement due to self-facilitation. We think that this mechanism is more appropriate in semi-arid and mesic savannas characterized

by a continuous vegetation cover, where herbivores can induce vegetation patterning through localized reduction of vegetation biomass and/or alteration of plant architecture. Hence, we hypothesize that the role of herbivores in pattern formation is of greater significance when the moisture availability increases, enabling herbivores to forage selectively while enhancing forage quality and regrowth. With increasing water availability, the vegetation can supply the herbivores with more forage, enabling a higher herbivore density that still induces vegetation patterning (i.e. Fig. 6 stretches out to the right). At very high levels of water availability, the vegetation is completely dominated by trees (Van Langevelde et al. 2003, Sankaran et al. 2005).

In this paper, we showed that herbivores at intermediate densities can induce spatial patterning in savanna vegetation through the interactions between self-facilitation and spatial dependency of foraging, with the type of pattern being influenced by the heterogeneity and dominant scale of the pre-existing vegetation. The findings presented here, and critical experimentation of their ecological validity, increase our understanding of heterogeneity and patterning in savanna vegetation, and the role of plant-herbivore interactions therein.

*Acknowledgements* – We wish to thank Marcella Oerlemans, Geerten Hengeveld, Hank Bartelink, Martijn Slot, Frederik Hengeveld, Anne-Marie van den Driessche and Frans Möller for their help during this research.

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