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6. TREE-GRASS COMPETITION IN SPACE AND TIME: INSIGHTS FROM A SIMPLE CELLULAR AUTOMATA MODEL BASED ON ECO-HYDROLOGICAL DYNAMICS†

ABSTRACT

Limiting water is considered to be a key resource in determining the composition and structure of savanna-ecosystems, which are characterized by a dynamical coexistence of trees and grasses. Despite this emphasis on the importance of hydrology, long-term fluctuations in rainfall have not been quantitatively incorporated in existing models of savanna functioning. In this study we present a simple cellular automata model in which death and reproduction chances of trees and grasses are based on the model outcome of a probabilistic eco-hydrological point model. The dynamical description of plant water stress is the determining factor for a tree-grass competition for space. The model was parameterised on the basis of data available for a Texas savanna. The model was run for different climatic situations, differing in mean annual rainfall and the year-to-year variability. Analyses were carried out for prolonged periods (up to 100000 years) to test the stability of the tree-grass coexistence. The spectra of the total number of trees and grasses showed a power-law signature representing fractal characteristics in time. The spatial behaviour of the model showed prolonged periods of tree clustering ended by periods of severe drought and a power law distribution of cluster sizes.

INTRODUCTION

Savannas are one of the major biomes of the world, and they are characterized by a coexistence of grasses and trees (Scholes and Archer, 1997; Bourliere and Hadley, 1970). Soil water availability is generally considered critical for determining the development of woody vegetation stocks (Fensham and Holman, 1999). Classical models suggest that limiting water is the key resource in determining tree densities, although other important variables like fire and grazing can maintain the population levels below their climatic equilibrium (Fensham and Holman, 1999; Belsky, 1990). Other variables like nutrient availability can be linked to the water limitations, as both mineralisation and transport of nutrients to the plant roots are strongly affected by water availability.

Despite this emphasis on the importance of soil moisture relations, long-term fluctuations in rainfall have not been incorporated in existing models of savanna functioning quantitatively. The models of Jeltsch et al. (1996 and 1998), which have drought as one of key features determining the savanna composition and

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structure, make no reference to real data. Furthermore, tree dieback measurements of the study of Fensham and Holman (1999) suggest that the model of Jetsch et al. (1996) may under-estimate either the magnitude of subsurface soil moisture deficits during extreme drought or the sensitivity of savanna tree species.

To increase the testability of spatial models describing savanna functioning, a quantitative coupling between rainfall, soil water availability and tree and grass functioning is necessary. This, however, is no trivial task. Recently, progress has been made in the description of the water balance dynamics of savanna-like systems at a point, including the linkage between climate, soil and vegetation (Rodriguez-Iturbe, 2000; Rodriguez-Iturbe et al., 1999a; Rodriguez-Iturbe et al., 1999b). Using the probabilistic description of soil water dynamics, a dynamical stress function was formulated that includes effects of the length of periods of water stress, the level of water stress and the frequency of the stress periods (Ridolfi et al., 2000; Porporato et al., 2000).

In this study this dynamical water stress function is taken as the basis to describe the death and establishment chances of trees and grasses in a simple spatially explicit model. Therefore, a description of the water dynamics at a point in space is the determining factor for a tree-grass competition for space, which always takes place at the local scale. The goal is to link tree-grass system functioning to measurable characteristics of growing season rainfall, such as the mean number of rainfall events per growing season and the mean rainfall depth per event. With the formulated model several tests were performed: First, the effects of rainfall amount and frequency on the spatial contest between grasses and trees were quantified. In this analysis large year-to-year variations in rainfall intensities were also included, one of the main climatological characteristics of savanna-ecosystems (Scholes and Archer, 1997). After this test the model was run for prolonged periods with the rainfall characteristics of the current climate in Texas. Both the temporal and spatial characteristics of the model output were analysed. The results are then discussed in relation to tree-grass coexistence and the quantitative testability of the model versus field measurements.

**DESCRIPTION OF THE ECOHYDROLOGICAL POINT MODEL**

A thorough description of the concepts and mathematics of the model can be found in Rodriguez-Iturbe et al. (1999a). Here only a synthesis is given with the most important features of the model.

The soil moisture balance equation at a point is written as

\[ n Z_r \frac{ds}{dt} = I(s,t) - E(s,t) - L(s,t) \]  (1)

With

- \( n \) porosity
$Z_r$  depth of soil  
$s(t)$ relative soil moisture content or saturation level  
$I(s,t)$ infiltration rate from rainfall  
$E(s,t)$ evapotranspiration rate  
$L(s,t)$ leakage or deep infiltration rate

Rainfall arrivals are assumed to be Poisson distributed with rate parameter $\lambda$. Every rainfall event has an associated depth $r$, characterized by an exponential distribution with parameter $\alpha$, where $1/\alpha$ is the mean depth of storms. The parameters $\lambda$ and $\alpha$ are assumed to be constant throughout time. The analysis is performed at a seasonal scale, which for the purpose of this paper may be thought of as the growing season of the region. In many cases it is convenient to distinguish between early and late growing season, each of them with their corresponding estimates of $\lambda$ and $\alpha$. The temporal structures of the storms are assumed to be concentrated at a point in time. Although the formulation is continuous in time, the interpretation of the water balance dynamics is at the daily timescale. Precipitation is thus modelled as an intermittent process of rainfall events, which arrive randomly in time with an average frequency of $\lambda$ events per day and an average depth described by the mean precipitation among the rainy days of a homogeneous season. The characteristics for the Texas savanna are, for example, $\lambda = 0.18$ day$^{-1}$ and $\alpha^{-1} = 1.5$ cm event$^{-1}$ for the growing season from May to September. The amount of rain that infiltrates into the soil from any particular storm is assumed to be equal to the depth of rainfall whenever there is enough storage available in the soil to accumulate the full depth. If rainfall exceeds the available volume runoff is generated; this is the mechanism of saturation from below, studied in detail by Dunne (1978). The infiltration into the soil is thus a random variable that depends on the climatic characteristics of the region as well as on the soil moisture at a site. Losses from interception, that is the part of the rainfall which is intercepted by vegetation and evaporates before reaching the soil, is incorporated by assuming a threshold for rainfall depth $\Delta$, below which no water effectively reaches the ground. Under this assumption the apparent rainfall process now occurs with a rate $\lambda' = \lambda e^{-\lambda\alpha}$ in which the depths have the same distribution as before (Rodriguez-Iturbe et al., 1999a).

Losses in (1) are from evapotranspiration and leakage. For a given plant the assumed dependence of evapotranspiration on soil moisture is given in Figure 1. In the interval between the hygroscopic point of the soil, $s_h$, and the wilting point of the plant only evaporation from the soil takes place. Above $s_w$ evapotranspiration increases linearly with soil moisture until it reaches a maximum value $E^*$, which takes place when moisture is above a threshold $s^*$. More realistically, the value of $E^*$ should be made dependent on the leaf area index and climatic characteristics like temperature, radiation and wind speed, but the representation of Figure 1 is considered appropriate at daily timescales under seasonally fixed conditions (Gardner and Ehlig, 1963; Spittlehouse and Black, 1981; Dunin et al., 1985). Like in the case of $\lambda$ and $\alpha$ it may be necessary to change the value of $E^*$ from the early to the late season. The moisture content $s^*$
represents the value below which stomata start restricting transpiration and the plant experiences water stress. For our purposes it is important that this gross approximation is not made blindly, and that both $E^*$ and $s^*$ reflect the type of vegetation at the site. Thus both $E^*$ and $s^*$ are different for the trees and grasses commonly found in savannas (e.g. typical values are $E^*$ around 4 mm day$^{-1}$ for trees and near 20% more for grasses). Although these parameters change with the specific vegetation, we will only distinguish between functionally different types, e.g. trees and grasses.

Losses from leakage are at maximum equal to the saturated conductivity of the soil $K_s$ when the soil is saturated ($s=1$). For $s<1$, leakage decreases following a power law, $K(s) = K_s s^d$, where the exponent $d$ depends on the type of soil (e.g., Clapp and Hornberger, 1978). The value of the field capacity, $s_{fc}$, at which leakage stops, of Figure 1 depends on the type of soil.

Laio et al. (2000) derived the equilibrium or steady state probability density function for soil moisture $p(s)$:

$$p(s) = \frac{C}{\eta_w} \left( \frac{s - s_h}{s_w - s_h} \right)^{\frac{\lambda (s_w - s_h)}{\eta_w} - 1} e^{-\lambda s}$$  \hspace{1cm} s_h < s \leq s_w$$

$$p(s) = \frac{C}{\eta_w} \left[ 1 + \left( \frac{\eta}{\eta_w} - 1 \right) \left( \frac{s - s_w}{s^* - s_w} \right) \right]^{\frac{\lambda (s^* - s_w)}{\eta - \eta_w} - 1} e^{-\lambda s}$$  \hspace{1cm} s_w < s \leq s^*$$

$$p(s) = \frac{C}{\eta} e^{-\lambda s} \left( \frac{\eta}{\eta_w} \right)^{\frac{\lambda (s^* - s) s^*}{\eta - \eta_w}}$$  \hspace{1cm} s^* < s \leq s_{fc}$$
\[ p(s) = \frac{C}{\eta} e^{-(\beta + \gamma)s + \beta \frac{w}{e} \frac{\eta e^{\beta \frac{w}{e}}}{(\eta - m) e^{\beta \frac{w}{e}} + m e^{\beta \frac{w}{e}}}} \frac{\lambda^t}{\beta(\eta - m)} + 1 \frac{\eta}{\eta_w} e^{\lambda^t \frac{s - s_w}{\eta_w} - \lambda^t (s - s_w)} 
\]

\[ s_{fc} < s \leq 1 \quad (2) \]

where

\[ \eta = \frac{E^*}{nZ_{r}} \quad \eta_w = \frac{E_w}{nZ_{r}} \]

\[ \lambda = \lambda e^{\alpha} \quad \gamma = \frac{nZ_{r}}{\alpha} \]

\[ m = \frac{K_s}{nZ_r (e^{\beta(1-s_w)} - 1)} \]

The constant \( C \) makes the area under the density equal to one, and is given explicitly in Laio et al. (2000). They show that the equilibrium probability density function and its moments vary drastically depending on climate, soil and vegetation characteristics.

**SOIL WATER STRESS**

In this study we incorporate the results of the above described point model for grasses and trees into a spatial model describing a competition for space. For this we couple the fitness of both trees and grasses at certain climatic situations (i.e. frequency and intensity of rainfall) to the amount of water stress they experience. We are therefore interested in the intensity, frequency and duration of the periods with water stress, i.e. excursions in \( s \)-values below \( s^* \). Porporato et al. (2000) derived a measure for the mean total vegetation water stress during a growing season. First, a ‘static’ value for the normalised water stress is defined, according to the function

\[ \zeta(t) = \left[ \frac{s^* - s(t)}{s^* - s_w} \right]^q \]

for \( s_w \leq s(t) \leq s^* \quad (3) \]

where \( 0 \leq \zeta(t) \leq 1 \), \( \zeta(t) = 0 \) for \( s > s^* \) and \( \zeta(t) = 1 \) for \( s < s_w \), and the exponent \( q \) accounts for the non-linear effects of water deficit on the plant functions.

The probability density function of \( \zeta \), denoted as \( p(\zeta) \) for \( s_w < s \leq s^* \) can be written as (Laio et al., 2000; Porporato et al., 2000)

\[ p(\zeta) = \frac{C_\zeta}{\eta_w} \left[ \left( 1 - \frac{\eta^*}{\eta_w} \right) \zeta^q + \frac{\eta}{\eta_w} \right]^{\lambda^t \frac{(s^* - s_w)}{\eta_w} - 1} \frac{1}{\eta^\gamma (s^* - s_w) \zeta^q - s^*} \]

where
The constant of integration \( C_\zeta \) in equation 4 can be deduced by imposing the condition

\[
\int_0^1 p(\zeta)d\zeta = P(s^e) - P(s_w)
\]  

(5)

where \( P(s^e) \) and \( P(s_w) \) are the values of the cumulative distribution function of soil moisture calculated in respectively in \( s = s^e \) and \( s = s_w \) (see Laio et al., 2000).

The mean ‘static’ water stress can then be calculated with:

\[
\bar{\zeta} = \int_0^1 \zeta p(\zeta)d\zeta + p(1)
\]  

(6)

The value \( \bar{\zeta} \) obviously also reflects those periods when \( \zeta \) is 0 and hence it is not very indicative of the actual vegetation conditions (Porporato et al., 2000). The mean value of water stress given that the plant is under stress is more meaningful. To obtain the latter only the part of the pdf of \( \zeta \) above zero has to be considered, thus obtaining for the mean

\[
\bar{\zeta}' = \frac{\zeta}{P(s^e)}
\]  

(7)

This value of ‘static’ water stress, representing the mean vegetation water stress during an excursion below \( s^e \), is then combined with the mean duration and the frequency of such excursions during the growing season, denoted respectively by the variables \( \overline{T_s} \) and \( \overline{N_s} \). This measure will be called the ‘dynamic’ water stress value, or mean total dynamic stress, \( \overline{\Theta} \), defined as

\[
\overline{\Theta} = \left( \frac{\zeta'\overline{T_s}}{kT_{\text{seas}}} \right) \frac{1}{\overline{N_s}} 
\]  

if \( \zeta' \overline{T}_s < kT_{\text{seas}} \)

\[
\overline{\Theta} = 1 
\]  

otherwise

(8)

The analytical form of the dynamic water stress is discussed at length in Porporato et al. (2000). Here we will only note that the function assumes a linear relationship between the mean time under stress, \( \overline{T}_s \), and the value of dynamic stress, \( \overline{\Theta} \), until a certain critical point at which the stress is at its maximum value. This value can also be considered the onset of permanent damage to the plant. The parameter \( k \) in Equation 8 allows to fix the value of this critical threshold: permanent damages appear when \( \zeta' \overline{T}_s > kT_{\text{seas}} \), with \( k \) representing
an index of plant resistance to water stress. The value of $k$ may also be interpreted as the average static stress $\zeta^*$ a plant can experience without suffering permanent damages, when the duration of the period of stress is the whole growing season. For a sensible definition of water stress it is also important to account how multiple periods of stress affect the plant status. The functional dependence of $\theta$ on $N_s$ is discussed at length in Porporato et al. (2000). For values of $N_s$ smaller than one, $\theta$ should increase with $N_s$. The value of $\overline{\theta}$ is then always below the value of $\frac{\zeta^* T_s}{kT_{seas}}$, which corresponds to the value of $N_s = 1$. In cases when $N_s > 1$, $\overline{\theta}$ should also increase with $N_s$, always being above the values corresponding to $N_s = 1$. Furthermore, the impact of large values of $N_s$ should be tempered in order to avoid erroneously high values of $\overline{\theta}$ for cases of very short but frequent stress periods. Other functional forms with similar behavior lead to analogous results.

The parameter values of the soil moisture point model are based on Rodríguez-Iturbe et al. (1999b) and Laio et al. (2000). For the grasses and trees used in this paper they are given in Table 1. The values of the dynamic stress as a function of the rate of arrivals of storm events, $\lambda$, are shown in Figure 2 for trees, grasses and tree seedlings using a mean event depth of 1.5 cm. The parameters of the point model are the same for trees and tree seedlings. To incorporate a higher sensitivity to severe drought for the tree seedlings, as compared to the mature trees, we adjusted the $k$-value in equation 8 from 1.0 (for trees) to 0.5 (for tree seedlings).

![Figure 2: Simulated dynamic stress-values as function of the $\lambda$-parameter ($\alpha' = 1.5$ cm event$^{-1}$)](image-url)
Table 1: The parameter values for trees and grasses used in the soil moisture point model

<table>
<thead>
<tr>
<th>Parameter name</th>
<th>Value trees</th>
<th>Value grass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zr [m]</td>
<td>1.0</td>
<td>0.4</td>
</tr>
<tr>
<td>N</td>
<td>0.43</td>
<td>0.43</td>
</tr>
<tr>
<td>Δ [cm event⁻¹]</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>s_w</td>
<td>0.18</td>
<td>0.17</td>
</tr>
<tr>
<td>s*</td>
<td>0.35</td>
<td>0.37</td>
</tr>
<tr>
<td>s_h</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>K_s [cm/day]</td>
<td>82.2</td>
<td>82.2</td>
</tr>
<tr>
<td>E* [cm/day]</td>
<td>0.442</td>
<td>0.476</td>
</tr>
<tr>
<td>Soil_evap [cm/day]</td>
<td>0.02</td>
<td>0.02</td>
</tr>
</tbody>
</table>

**Spatial Model**

In the spatial model trees and grasses compete for the available space. Their death and propagation rates are directly linked to the growing season values of the dynamic stress function described above. There is therefore no explicit spatial competition for water, like in Rodriguez-Iturbe et al. (1999a), but only a dynamical competition for space based on water dependent vegetation stress.

A cellular automata model is defined in a grid of 100 by 100 cells. The cells are considered to have the canopy size of one individual mature tree, about 25 m². There are three possible configurations for a cell: it can be occupied by a tree, by tree seedlings, which are trees in the age of 1 to 5 years, and by grasses. There is no mixed occupation possible in a cell. A tree seedling cannot reproduce, and after 5 years it becomes a mature tree. Periodic boundary conditions are assumed throughout the simulation in order to prevent border effects.

Death is modelled very simple. The chances of death for trees, tree seedlings and grasses were defined by the value of dynamic stress minus a threshold value. In this manner a minimum of dynamical stress does not immediately lead to an increase in death chances, which would be a gross over-estimation of the sensitivity of trees and grasses to water stress. The maximum values of tree and seedling death, occurring at severe water stress, are based on the higher values presented in the study of Fensham and Holman (1999), thereby determining the values of the threshold parameters. The parameter values are given in Table 2. Also a minimum death chance is used, in the absence of ‘damaging’ water stress (i.e. the value of the dynamic water stress is below the threshold value), see Table 2. Death occurred randomly in space, no sheltering effects or whatever other spatial effects on death chances are taken into account.

Settlement of tree seedlings or grasses can only take place in empty cells. Of an empty cell the 24 nearest neighbour cells are potential colonizers (the first ring of 8 neighbours, and the next ring of 16 neighbours). From this neighbour-
Table 2: The parameter values for trees, tree seedlings and grasses used in the dynamic stress function and the spatial model

<table>
<thead>
<tr>
<th>Parameter name</th>
<th>Value trees</th>
<th>Value tree seedlings</th>
<th>Tree</th>
<th>Value grass</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dynamical stress function</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>1.0</td>
<td>0.5</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td><strong>Spatial model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Threshold value</td>
<td>0.6</td>
<td>0.45</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td>Minimum death chance</td>
<td>0.01</td>
<td>0.05</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>Maximum settlement probability</td>
<td>0.75</td>
<td>0.05</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>Onset of zero settlement probability</td>
<td>0.1</td>
<td>(0.7 without threshold)</td>
<td>0.2  (i.e. 0.43 without threshold)</td>
<td></td>
</tr>
</tbody>
</table>

Hood one of the cells occupied by either trees or grasses is selected at random. If a tree occupies the cell, there is a possibility of settlement of a tree seedling in the empty cell depending on the value of dynamic water stress of trees for that particular growing season. If the cell is still empty after this calculation or if the randomly chosen cell was not occupied by a tree, there is possibility of grass settlement in the empty cell. This also depends on the value of the dynamic water stress of grasses. Therefore, for grasses it was not strictly necessary to be present in the neighbourhood of an empty cell in order to colonize the space. The probabilities of settlement of trees and grasses as a function of the dynamic stress minus the same threshold parameters as defined for the death chances (i.e. which have different values for grasses and trees) are given in Figure 3. The parameter values of the functions are given in Table 2. The optimal values of tree and grass settlement are based on the values of Jeltsch et al. (1996).

Figure 3: The chances of settlement in the spatial model of trees and grasses as function of dynamic stress minus the threshold value (for trees 0.60 and for grasses 0.23)
Figure 3 shows the difference in sensitivity and maximum probabilities of settlement for trees and grasses. If the stress threshold is not exceeded, trees have the highest probability of settlement because of their massive local seed distribution. However, with the occurrence of stress the settlement probability decreases much faster than that of grasses because of the higher drought sensitivity of both the seed production and the seed settlement of trees versus grasses. Grasses have a much more diffuse seed distribution (and therefore in the model also settlement of grasses can take place if no grass neighbour is present) and lower settlement chances compared to trees in the no-stress situation. The difference in drought stress sensitivity was based on the measurements in Texas, which showed an increase in tree density in wet years, and a decrease in dry years (Archer et al., 1988).

The spatial model therefore consisted of 3 threshold parameters for the dynamic stress function, 4 propagation and settlement parameters (2 for trees and two for grasses), and 3 minimum values of death chance. In total there were 10 parameters in this simple spatial model (see also Table 2). Depending on the value of a certain cell, whether tree, tree seedling or grass, the parameters are assigned to that cell. No further spatial interactions, resulting in adjusted parameter values effected by neighbourhood cell values, are included in the model.

**MODEL TESTING**

The spatial model is tested both by its global outcome, the number of trees, tree seedlings and grasses present throughout time, and by the spatial patterns it generates.

First, the sensitivity to the amount of rainfall is tested. This is done by changing the λ-value from very low to high values. The model is run for three thousand years with the same rainfall-input, and the numbers of trees and grasses throughout the last 1000 years are studied in detail. The simulation period is chosen so long in order to avoid transients, and to be able to select a long time period over which the model outcome can be evaluated for the different runs.

As one of the main characteristics of savanna ecosystems is the high variability in inter-annual rainfall amounts, an analysis with year-to-year varying rainfall amounts was also undertaken. This is done by assuming growing seasons with λ and α parameters gamma distributed, as is frequently found in climatological data (e.g., D'Odorico et al., 2000). At a certain run of 3000 years each year a random value of λ and α is sampled from their respective distributions. The 2 parameter gamma distributions are characterized by their mean value and standard deviation. Similar to the former analysis also here a range of λ and α-values are tested. Thus, to investigate the effects of the year-to-year variation of rainfall, several values of the standard deviations applied to the λ and α-distributions were tested.
After these sensitivity tests, the model was run for 100000 years at current climate conditions in Texas. The coefficients of variation of $\lambda$ and $\alpha_1$ are set at 0.2 and 0.3, respectively. These are values in the modest part of the range of year to year variability recorded by the Texas weather stations (Porporato et al., 2000). Both the temporal and spatial characteristics of the model output are then analysed. The temporal series of the rainfall input and the corresponding vegetation output are studied via their power spectra complemented with auto- and cross-correlation analyses.

The spatial fields of the model are analysed using three characteristics. First, for a consecutive set of 1500 years the spatial distribution of the trees is tested for spatial clustering by applying Ripley’s $K$-function (Ripley, 1976; Haase, 1995; Wiegand et al., 1998). Of each spatial field an inner plot of 70 by 70 cells is selected. On this plot the univariate form of Ripley’s $K$-function is applied. In the univariate case the clustering or hyperdispersion of a set of points in a circular area around the points of a certain pattern (in our case trees), is estimated through comparison with the expected values for a randomly distributed field. The approximately unbiased estimator for $K(l)$, where $l$ is the radius of the circular area (also called the length scale), is (Ripley, 1976)

$$
\hat{K}(l) = n^{-2} A \sum_{i \neq j} w_{ij}^{-1} I_i(u_{ij})
$$

where $n$ is the number of events (trees) in the analysed field, $A$ is the area of the field, $I_i$ is a counter variable, $u_{ij}$ is the distance between the events $i$ and $j$, and $w_{ij}$ is a weighting factor to correct for edge effects. For all events where $u_{ij} < 1$ the counter variable $I_i$ is set to one, otherwise it is set to 0.

With an inner field of 70 by 70 cells, one may apply a maximum radius of the circular area of 15 cells without using edge-corrections (Haase, 1995). To test whether the trees in the fields simulated by the model show significant departures from a random pattern, we estimate the 95% confidence interval around the expected values for $K$ in the case of a random pattern, using randomly filled fields with the same density as the trees have in the field that was tested (Haase, 1995). By comparing the maximum and minimum $K$-value of the randomisation procedure with the values obtained for the field under analysis, the significance of the departure from the null hypothesis of random distribution may then be tested (Haase, 1995; Wiegand et al., 1998).

The second spatial characterisation of the simulated fields is based on the calculation of the cluster size distributions. For 100 fields, separated from each other by a simulation time of 100 years, the sizes of the tree clusters are calculated. As the value of size we take the so-called ‘mass’ of the clusters (Stauffer and Aharony, 1992), which is number of members of a certain cluster. To test the possible existence of a power law distribution, the number of clusters larger than a certain size is plotted versus the cluster size, on a log-log scale. The 8 direct neighbours of certain tree-cell may belong to the same cluster in case they are also occupied by a tree.
The probability distribution of cluster sizes is also studied separately for two types of simulated fields: those which have an increment in tree density in the previous $\Delta t$ and those which show a decrease in tree density. In this way the effects of the totally random occurrence of tree death on the cluster size distribution can be tested.

The third test deals with the percolation characteristics of the model outputs: is it possible to reach the upper boundary of the model field starting from the lower boundary, and travelling only through cells occupied by trees or tree seedlings. Percolation is analysed under the assumption that from one cell all eight neighbours can be reached. The results of the fields simulated by the model are then compared with results derived from the randomly filled fields.

**RESULTS AND DISCUSSION**

**Rainfall sensitivity**

The combined effects of increasing rainfall and year-to-year rainfall variability are shown in Figure 4. In the case of no year-to-year variation for $\lambda > 0.11 \text{ d}^{-1}$, the tree population becomes sustainable and shows a sharp increase from a cover of zero percent to a cover of nearly 50 percent. For $\lambda$'s between 0.115 and 0.12 the tree population shows a small decrease in density. This is caused by the fact that at these $\lambda$'s, trees do not experience major water stress (the value of the dynamic stress value is below their threshold), whereas the tree seedlings are still under high stress conditions (see Figure 2). Because the water stress of the grasses decreases in this range of $\lambda$-values, the density of grasses increases, and as only limited space is available it does so at the expense of seedlings. For $\lambda$'s above 0.12 rainfall events per day, the dynamic stress of the tree seedlings also decreases, and the density of the trees increases sharply again.

The above effect totally disappears when year-to-year variation is included in the rainfall amounts. When inter-annual rainfall variation is present, trees are absent in the lower range of $\lambda$'s, and then increase rapidly in density over a relatively small interval of $\lambda$. The $\lambda$-value at which the tree population becomes sustainable becomes higher with increasing year-to-year variability. Also visible in Figure 4 is the increase in the standard deviations of tree and grass densities in the last thousand years of the simulation at increasing year-to-year variation in rainfall amounts. With increasing rainfall variability, very dry years occur more often, resulting in high tree and grass kill-off, and thereby prohibiting the occurrence of only trees in the model at higher $\lambda$-values. The increasing year-to-year variability therefore shows a tendency to increase the interval of tree-grass coexistence, in which over a broader range of $\lambda$-values the grasses are present in significant amounts, especially considering the increased standard deviation. Values of the year-to-year variations in rainfall larger than those shown in Figure 4 were not considered, because the populations of trees and grasses are then still
Figure 4: The mean and standard deviations (bars) of the last 1000 years of a model run of 3000 years of cell coverage of trees (including tree seedlings) and grasses as function of λ (λ = 1.5 cm event⁻¹); cov = coefficient of variation (std0: cov-λ = 0.00 and cov-α¹ = 0.000; std1: cov-λ = 0.05 and cov-α¹ = 0.025; std2: cov-λ = 0.10 and cov-α¹ = 0.050; std3: cov-λ = 0.15 and cov-α¹ = 0.075; std4: cov-λ = 0.20 and cov-α¹ = 0.100). 

in transient behaviour after 3000 years, and the randomly rainfall characteristics have a large effect on the mean value of the last 1000 years.

The results show that coexistence between grasses and trees in the model occurs at rainfall values at which the death rate of trees is high enough to prevent a total dominance and low enough to keep the tree population sustainable. Coexistence of numerous plant species competing for a single limiting resource can be accounted for in classical ecological models that are spatially explicit if a trade-off exists in colonization, competition and longevity (Tilman, 1994). Disturbance is a key factor for this trade-off, because it assures the availability of free places where settlement of one or the other species can occur. In this model periods of severe water stress cause death of trees and especially tree seedlings, thereby giving grasses the opportunity for settlement. In periods with high rainfall amounts the trees take over because of their lower overall death rate and their higher settlement chance (see Figure 3) at low water stress than those for grasses. Although a difference in rooting depth based on Texas data was used in the point model (see Table 1), it was not the key factor determining coexistence because no competition for water was incorporated into the model. A better, field-based estimate of the death parameters of both grasses and trees could answer the question whether disturbance is the determining factor for tree-grass coexistence in savanna-ecosystems as suggested by this model or whether a niche separation by rooting depth as assumed by the so-called Walter hypothe-
Figure 5: Model input (as 10-years running average of rainfall) and output (percentage coverage of trees and grasses) for a model-run of 5000 years ($<\lambda> = 0.18$ d$^{-1}$ and a cov of 0.2, and $<\alpha'> = 1.5$ cm event$^{-1}$ and cov of 0.3).
sis (Scholes and Archer, 1997; Walter et al., 1971), assuring different sources of water-use for trees and grasses, is also necessary.

Figure 5 shows a run of 5,000 years using rainfall parameters like those representative for the La Copita Research are in Texas (Archer et al., 1988), \(<\lambda>=0.18 \text{ d}^{-1}\) and a coefficient of variation of 0.2, and \(<\alpha^1>=1.5 \text{ cm event}^{-1}\) with a coefficient of variation of 0.3 (Porporato et al., 2000). The first 500 years were removed to avoid transient effects. The results show a dynamical coexistence between trees and grasses, although trees undergo prolonged periods of low densities. In a dryer climate therefore, or with a lower tree threshold for the dynamic stress, the trees will die out. Also when the year-to-year variance is increased, using for example the same \(<\alpha^1>\), but with a coefficient of variation of 0.4, the trees die out after about two or three thousand years. However, the increase in the occurrence of dry periods can be easily compensated, by increasing the threshold value for tree dynamic water stress. In these experiments the maximum tree death, defined by the tree threshold value, is at the higher values of the ranges given by Fensham and Holman (1999). Again it is clear that a field-based estimate of tree death chances is essential for a reliable model parameterisation.

Figure 5 also clearly shows that if trees/grasses have a high density, grasses/trees have a low density. A strong coupling is present between the values of the ten-year running average of rainfall and the tree density. If 10-year averaged rainfall is low then severe tree die back will occur, and if the 10-year averaged rainfall is high then in most cases an increase of trees is clearly visible.

**Time series analysis**

Figure 6 shows the results of the power spectrum analysis. As expected the spectrum of the rainfall input is flat over the whole frequency range, but model outputs show considerable structure over all frequencies. Most clearly, the power spectra of the density of coverage of grasses and bare soil show a power law relation over an extended frequency range. Thus local interactions based on the water stress present at each site lead to temporal structures when the system is driven by simple white noise. Power law power spectra in time are a typical signature of temporal fractal signals, which display long term dependence.

The spectra the density of coverage of trees and tree seedlings show departures from power law dependence of frequencies. The trees show peaks at frequencies of about 1/2.5 years and 1/5 years, whereas the tree seedlings show peaks at frequencies of about 1/3 years and 1/8 years. These peaks are likely to results from dynamic effects arising from the 5-year interval chosen as seedling lifetime. Notice that the spectrum for trees and tree seedlings together does not show the above behaviour.

Figure 7 shows the results of the auto-correlation analysis of the densities of vegetation coverage. Both trees and tree seedlings show the lowest correlation values over the longer time scales which is not surprising because of the five
Rain

Trees & Tree seedlings

Trees

Tree Seedlings

Grass

Bare Soil

Figure 6: Power spectral density plots of the density of cell coverage derived from a model run of 100000 years (the rainfall characteristics are the same as in Figure 5)

year seedling stage in the model. This stage is one of increased sensitivity to drought, thereby leading to a high variability in the number of seedlings that transform to trees each year. This variability is most strongly reflected by the model in the number of bare soil cells. The number of grass cells is much more stable in time because of only an indirect relation with the number of trees and tree seedlings, and the absence of a seedling stage.

The cross-correlations of Figure 8a clearly show the competition for space between the trees and the grasses. The lag zero correlation value is low com-
Figure 7: Autocorrelation plot of the density of cell coverage derived from a model-run of 100000 years (the rainfall characteristics are the same as in Figure 5)

pared to correlations with lags up to 500 years (for values higher than 500 years the correlation values decrease again). Also the cross-correlation between trees and trees seedlings in Figure 8b shows a minimum for low time lags. The correlation shows a clear peak at -5 years, indicating strong linear dependence between trees at the current time value and the number of tree seedlings five years earlier. Another peak, although smaller, is visible near +10 years, thereby showing a stronger relation between trees at current time with tree seedlings ten years later.

Figure 8: Crosscorrelation plots of the density of vegetation coverage derived from a model-run of 100000 year (the rainfall characteristics are the same as in Figure 5)
Figure 9: Results of Ripley's K-function together with percentage tree cover (500 years in advance of the presented run were removed to prevent effects of initial conditions; the rainfall characteristics are the same as in Figure 5)
Spatial pattern analysis

For a smaller number of years we calculated Ripley’s K-function, and tested whether there was significant clustering present in the spatial tree distributions. These tests do not include tree seedlings because given the pattern of seedling settlement, i.e. close to the mature trees, the spatial distribution of both trees and tree seedlings will always show significant clustering, and therefore is not very illuminating. The results of the tree distributions are shown in Figure 9; also here the initial 500 years were deleted from the model outcome to remove effects of model initialisation. In the upper graph the significant departures from the random distributions are shown for a length scale of 2 to 16. Clearly visible are prolonged periods in which significant clustering occurs at several length scales. These periods are finished when a major tree die back occurs caused by severe drought. As tree death occurs in a spatially uncorrelated pattern, this leads to a breakdown of the clusters present, and therefore causes the disappearance of significant spatial clustering. The clustering increases in length scales at periods in which there is an increase in tree density. This may be explained by the fact that tree seedling establishment can only occur in the neighbourhood of mature trees. When the seedlings become mature trees, the spatial distribution of these is strongly clustered around the trees whose ‘seeds’ lead to the original establishment.

In Figure 10 two fields are shown that have about the same tree density (~15 %) but differ totally in their cluster characteristics (Field 1 and Field 2 in Figure 9). In Field 2 significant clustering is present at all 15 length scales of Ripley’s K-function. Clearly visible are isolated patches of trees separated by grass vegetation and bare soil. In Field 1 the spatial tree distribution is not significantly different from a random one. As shown in Figure 9, Field 1 occurs just after a severe tree die back (and also grass die back) and thus the density of bare soil cells is much higher than in Field 2, which occurs in a period in which tree densities are increasing. The model, although very simple, can yield totally different spatial distributions, even at the same level of vegetation density.

Figure 11 shows the frequency of occurrence of clusters of different sizes for trees and seedlings. There exists an approximate power law distribution of cluster sizes, except for very small and very large clusters. The deviations at the two extremes may be impacted by the smaller sample size for these ranges as well as for finite size effects of the domain in the case of the large clusters. The steepness of the power law for the case of trees-only analysis is smaller than for the case of both trees and seedlings. This is caused by the fact that in the latter case the number of large clusters is much higher than in the tree only-analysis, and the number of small clusters is lower.

In Figure 12 the cluster-size distribution for trees is plotted distinguishing between fields that show an increase of trees in time, and fields that show a decrease of trees in time. The number of fields obtained when trees decrease in the previous year is smaller than the number of fields obtained with an increase of trees in time: of the total of 140 field, 90 fields are ‘increase’ fields, and 50 are ‘decrease’ fields. This implies that most of the time, as can also be seen in
Figure 10: A: Spatial field No. 1 of Figure 9
B: Spatial field No. 2 of Figure 9
(for explanation see text)
Figure 11: Cluster-size distributions of 200 fields of model output (N is number of fields, A is cluster-size)

Figure 12: Cluster-size distribution of the tree model output separated into fields obtained at temporal increasing (i.e. positive) and decreasing (i.e. negative) tree cell coverage
Figure 13: Percolation characteristics of model in time, together with tree and tree seedling cell cover
Figure 14: Percolation characteristics of model compared to those of random fields of same size and cell cover.

Figure 5, trees were increasing in density, and decreases in tree density occurred in relatively short time spans of severe drought. The distribution of the ‘decrease’ fields distribution shows a higher slope than that of the ‘increase’ fields: the ‘decrease’ fields therefore had relatively more small clusters, caused by the spatially uncorrelated tree death that occurs at the moment the field is analysed.

The above results suggest that as clustering of trees is observed on a mosaic of grasses and bare soil, the distribution of cluster sizes is an important criterion in the quantification of the observed patterns. Moreover, the possible existence of power laws in these distributions signals the likely presence of a fractal structure in the spatial vegetation pattern.

Figures 13 and 14 show the results of the percolation analysis. Percolation only occurred when the tree and tree seedling density was high enough. For infinite lattices where each site has the same probability of being occupied the theoretical density at which percolation takes place is 40.72 % (Stauffer and Aharony, 1992). The relation between density and the occurrence of percolation is less clearly defined in simulations with the present model and in fact it can be attained with tree densities as low as 32 % or as high as 52 %.

Field measurements and modelling challenges
The results presented in this paper are purely model results. How can they be linked to field measurements to test the model? The temporal evolution of the model outcome is very difficult to test, because it is heavily dependent on the initial condition that is used (see for example Figure 5). Thus the dynamics in time differ greatly when the model is started at a high tree density or when it is started with a low tree density.
Figure 5 also shows the high temporal dynamics of the model output: tree density can increase up to 50% in less than 50 years when the climatic conditions are favourable for tree settlement. These high dynamics are also present in measurements done by Archer et al. (1988): in 1941 the woody plant coverage was 13%, in 1960 (after a severe drought period) it was 8% and in 1983 it was 36%. The woody plant coverage therefore increased in about 20 years almost 30%!

Another way to test the model is to compare cluster size distributions predicted by the models with measurements in the field. This model output is robust and not affected by the stochastical character of the model: each time the model is run, the same slope of the cluster size distribution is found. Probably the results of the model will deviate strongly from the measurements: death is simulated in the model as a spatially random process, which is probably a gross simplification of the real process. Furthermore no spatial competition for water is included in the model, let alone effects of fire and nutrients.

A major research and modelling challenge for the future will be the quantitative exploration of the spatial and temporal behaviour of savanna systems. This model is a first attempt to achieve a quantitative linkage between rainfall and tree and grass interactions, and to increase the testability of these kinds of models on data of field measurements. Competition for space and the impact of inter-annual climatic variations may be studied through this type of scheme. The model is kept simple with a low number of parameters, to increase the possibilities for parameterisation. Complex models like Higgins et al. (2000) result in high numbers of parameters, which are very difficult to estimate, and are thereby not suited for application over ranges of savanna-like systems. Although extremely simple, the spatio-temporal model presented here is the first attempt to objectively link the probabilities of colonisation and death of functionally different types of vegetation in terms of their dependence on varying climatic conditions. The results obtained agree quite well with the type of temporal and spatial patterns observed in savanna ecosystems.

REFERENCES


