Tree-grass competition in space and time: Insights from a simple cellular automata model based on ecohydrological dynamics

Mark T. van Wijk
Physical Geography and Soil Science, Institute of Biodiversity and Ecosystem Dynamics (IBED), Universiteit van Amsterdam, Amsterdam, Netherlands

Ignacio Rodriguez-Iturbe
Department of Civil and Environmental Engineering and Princeton Environmental Institute, Princeton University, Princeton, New Jersey, USA

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[1] Water is a key resource in determining the composition and structure of savanna ecosystems. In this study we present a simple cellular automata model in which death and reproduction chances of trees and grasses are based on the dynamical description of plant water stress by a probabilistic ecohydrological point model, using the parameterization for a Texas savanna. The results show that the model behavior, despite its simplicity, can be linked to ecological reality: the model yields a dynamic tree-grass coexistence driven by the annual rainfall, and the space-time behavior shows that both random and clustered tree distributions for periods up to 100 years can be observed. Both temporal and spatial model output display fractal characteristics suggesting the possibility of a self-organized critical dynamics. Thus power law behavior is observed in both the spectral density function and the cluster size distribution. The presence of spatial fractal characteristic opens avenues for more thorough model testing. INDEX TERMS: 1851 Hydrology: Plant ecology; 1869 Hydrology: Stochastic processes; 1866 Hydrology: Soil moisture; 1812 Hydrology: Drought; KEYWORDS: cellular automata, drought, plant ecology, competition, ecohydrology


1. Introduction

[2] Savannas are one of the major biomes of the world, and one of its characteristics the coexistence of grasses and trees [ Scholes and Archer, 1997; Bowler and Hadley, 1970]. Soil water availability is generally considered critical for determining the development of woody vegetation [ Fensham and Holman, 1999]. Classical models suggest that 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]. In the case of southern Texas, changes in livestock grazing and fire regimes appear to be important forces behind the increase of woody plant abundance. Nevertheless, vegetation changes in this region are highly punctuated by variations in precipitation. Thus the decrease in total woody plant cover in the 1941–1960 drought was followed by a threefold to eightfold increase during the above normal annual rainfall period between 1960 and 1983 [ Archer et al., 1988].

[3] Despite the well-known importance of soil moisture effects on vegetation dynamics, long-term fluctuations in rainfall have not been quantitatively incorporated in existing models of savanna dynamics. The models of Jeltsch et al. [1996, 1998], which have drought as one of key features determining the savanna composition and structure, make no reference to real data. Furthermore, tree dieback measurements of the study of Fensham and Holman [1999] suggest that the model of Jeltsch et al. [1996] may underestimate either the magnitude of subsurface soil moisture deficits during extreme drought or the sensitivity of savanna tree species.

[4] To increase the quantitative testability of spatial models describing savanna functioning, a mechanistic 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 et al., 1999a, 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., 2001].

[5] 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. Thus the probabilistic dynamics of the soil water content is the determining factor for a tree-grass competition for space, which always takes place at the local scale. The success of a species in a particular environment depends on
three different aspects: its ability to survive adversity, its ability to compete for limited resources and its ability to efficiently convert these resources into growth [Scholes and Walker, 1993], in which the term “efficient” is linked to the ability of a species to have a high value for the units growth divided by the units of resource used, in a certain time interval. Survival and competitiveness are crucial in water-limited ecosystems, while efficiency is the key in wet environments. In all cases, nutrients are essential and in water limited ecosystems the mineralization and uptake of such nutrients is controlled by the dynamics of soil water.

To achieve a quantitative linkage between measured rainfall and ecohydrological interactions a simple cellular automata model is developed and explored. The goal of this study is not to incorporate all components of the interactions between ecology and hydrology, which would lead at this moment to model structures which are very difficult to parameterize, but a simple model to test to what kind of temporal and spatial behavior such a model can lead. The model itself and the model results are discussed in relation to the ecological and hydrological processes incorporated, and ignored, in the model structure. Aspects of the model that are discussed may be grouped along three different categories. First, the validity of the model: what is the relation between model behavior and ecological reality. Can the model describe stable coexistence between grasses and trees over prolonged periods of time? Can it describe spatial patterns found in the field? Second, what is the temporal and spatial behavior of the model? Can this stochastic model, driven as it is by the chance processes of life and death of trees and grasses, result in some characteristic statistical output signature that is obtained throughout different model runs? Formulated in another way: is there robust model output that can be used to test this stochastic model versus field measurements? Third, how can field measurements be used to test and improve this simple model, and what are the most important modeling challenges?

2. Point Model Description

In the spatial model trees and grasses compete for the available space. Their death and colonization rates are directly linked to the growing season values of a dynamic stress function derived for the ecohydrological point model described by Rodriguez-Iturbe et al. [1999a]. Here we will only give a short summary of the model, discussing the processes incorporated and their parameterization in the model.

The basis of the model is the soil moisture balance equation at a point, written as

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

with

- \( n \) porosity;
- \( Zr \) effective 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 is assumed to be a marked Poisson process in time, characterized by the rate of storm arrivals, \( \lambda \), and the depth of each event, which follows an exponential distribution with mean \( \alpha^{-1} \). Analysis of the model is performed at a seasonal scale, which for the purpose of this paper may be thought of as the growing season of the region. 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. Interception is incorporated by a constant rainfall threshold, which is subtracted from the amount of rain reaching the ground. Transpiration is made dependent on soil water content as shown by Rodriguez-Iturbe et al. [1999a]. Below a certain threshold value, transpiration decreases linearly with soil moisture until the wilting point, where it ceases. Average daily maximum transpiration, \( E_{\text{max}} \), represents the daily transpiration losses under well-watered conditions and is considered constant throughout the season. More realistically, the value of \( E_{\text{max}} \) should be made dependent on the leaf area index and climatic characteristics like temperature, radiation and wind speed, but the representation is considered appropriate at daily timescales under seasonally fixed conditions [Gardner and Ehlig, 1963; Spittlehouse and Black, 1981; Dunin et al., 1985]. If necessary, the values of \( \alpha \), \( \lambda \), and \( E_{\text{max}} \) may be estimated separately for the earlier and the later part of the growing season. Leakage is modeled as dependent on soil water content [Rodriguez-Iturbe et al., 1999a; Clapp and Hornberger, 1978]. Salvucci [2001] obtained an excellent comparison between the analytical probability function of soil moisture derived for the previous models by Rodriguez et al. [1999a] and the historic data at Illinois.

In the spatial model we want to link the water stress experienced by the vegetation to the vegetation reproduction and death. We are therefore interested in the intensity, frequency and duration of the periods with water stress. In the work of Porporato et al. [2001] a measure for the mean total vegetation water stress during a growing season is derived based on all three afore mentioned characteristics of the periods of water stress. A synthesis of the dynamic water stress formulation is given in Appendix A. Notice that it involves a factor \( k \), which can be interpreted as the average value of stress a plant can experience without suffering permanent damages, when the duration of the period of stress is the whole growing season. In this parameter therefore the drought tolerance of different species can be accounted for.

The parameter values of the soil moisture point model are given by Rodriguez-Iturbe et al. [1999b] and Laio et al. [2001a] for climate and soil types present in a savanna in southwestern Texas. For the grasses and trees used in this paper they are given in Table 1. Differences between grasses and trees are incorporated in the rooting depth (deeper for trees), the interception parameter (higher for trees), the \( E_{\text{max}} \) values and in the value of soil water content at which soil water stress begins to occur [Laio et al., 2001a, 2001b]. The abiotic 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 stress sensitivity parameter “\( k \)” (see equation A6) from 1.0 (for trees) to 0.5 (for tree seedlings). This decrease of the \( k \) parameter results, using the same rainfall characteristics, in
3. Spatial Model Description

[1] In the spatial model, trees and grasses compete for the available space and not for the available water like in the work of Rodriguez-Iturbe et al. [1999a]. Their death and propagation rates are directly linked to the growing season values of the dynamic stress function described above and more elaborately in Appendix A.

[14] A cellular automata model is defined in a grid of 100 by 100 cells, where the status of each cell is updated at every time step depending on the status of its neighbors. In this way spatial explicit interactions can be easily incorporated. The cells are considered to have the canopy size of one individual mature tree, about 25 m². There are four possible configurations for a cell: it can be unoccupied or it can be occupied by a tree, by tree seedlings, which are trees in the age of 1–5 years, and by grasses. In this simple cellular automaton approach no mixed occupation is possible in a cell. In the case of a cell occupied with tree seedlings, which is in reality very likely to be also occupied by grasses, the implicit assumption thereby is that if tree seedlings survive, despite their higher death probability due to a higher sensitivity to water stress and high competition, they will outcompete the grasses while growing larger and winning the competition for light. 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 boundary effects.

[15] For each cell depending on the cell status (e.g., empty, tree, tree seedling or grass) the point model with the corresponding parameterization is run, which thus gives the value for the dynamic stress at that site. The spatial model incorporates no spatial heterogeneity in the abiotic components of the model: rainfall is distributed evenly over the total grid, all soil physical parameters used in the point model are the same, and no spatial redistribution of runoff water takes place. The spatial model output in terms of water redistribution is therefore likely to be oversimplified, and all patterns that do arise in the spatial vegetation output of the model are therefore determined by the biotic part of the model: death and reproduction. In further studies the effects of spatial heterogeneity in soil physical characteristics and water redistribution will be analyzed, but as a first step, we analyze the effects of biological spatial heterogeneity here first. Our goal is not to reproduce realistic future scenarios of the spatiotemporal vegetation structure for the savannas of southern Texas. Rather the goal is the exploration of the impact of long-term interannual rainfall

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**Table 1. Parameter Values for Trees and Grasses Used in the Soil Moisture Point Model**

<table>
<thead>
<tr>
<th>Parameter Name</th>
<th>Trees Value</th>
<th>Grass Value</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>$\Delta$, cm</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>$s_r$</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>$s_{sw}$</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>$K_e$, cm d⁻¹</td>
<td>82.2</td>
<td>82.2</td>
</tr>
<tr>
<td>Emax, cm d⁻¹</td>
<td>0.442</td>
<td>0.476</td>
</tr>
<tr>
<td>Soil_evap, cm d⁻¹</td>
<td>0.2</td>
<td>0.2</td>
</tr>
</tbody>
</table>

*Variables are as follows: Zr is rooting depth, N is porosity of soil, $\Delta$ is rainfall interception threshold, $s_r$ is the relative soil moisture at plant wilting point, $s$ is relative soil water content from which maximum evapotranspiration occurs, $s_{sw}$ is the hygroscopic point, $K_e$ is the saturated hydraulic conductivity, Emax is the maximum average daily transpiration rate, and Soil_evap is daily soil evaporation.*
fluctuations on some key issues of the tree-grass structure of savannas.

[16] Death and reproduction of both trees and grasses are modeled very simply. The chances of death for trees, tree seedlings, and grasses are defined by the value of dynamic stress minus a threshold value. In this way death chances are directly linked to the water stress experienced by the vegetation. By incorporating a threshold, a minimum of dynamical stress will not immediately lead to an increase in death chances, which would be a gross overestimation of the sensitivity of trees and grasses to water stress. It is important to point out the fact that trees and grasses have several mechanisms through which water stress can be avoided or diminished, like leaf area index adjustment. These avoidance mechanisms are implicitly incorporated in the model by the use of a maximal death probability, i.e., when the dynamic water stress is equal to one, which is much smaller than one. The maximum values of tree and seedling deaths, occurring at severe water stress, are based on the 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 occurs randomly in space, with no sheltering effects or whatever other spatial dynamics on death chances being taken into account.

[17] The spatial distribution of tree seedlings and grasses are considered different from each other. We assume after Jeltsch et al. [1996] that the distribution of tree seeds is more localized than the distribution of grass seeds. This difference, which is gradual in the field, is in the model rather abrupt for simplicity reasons: only the nearest 24 neighbors of a mature tree are available for tree settlement. To represent the fact that reproduction is affected already at relative low values of water stress compared to effects of drought stress on mortality, the settlement chances decrease over a relative small range of dynamic stress values from 1 to 0: for trees at dynamic stress values minus the threshold from 0 to 0.1, and for grasses at dynamic stress values minus the threshold value from 0 to 0.2.

[18] Colonization is modeled as follows: settlement of tree seedlings or grasses can only take place in empty cells. The 24 nearest neighbor cells of an empty cell are potential colonizers (the first ring of 8 neighbors, and the next ring of 16 neighbors). From this neighborhood 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 is not strictly necessary to be present in the neighborhood 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 2. The parameter values of the functions are given in Table 2. The maximum values of the settlement probabilities for trees and grasses are based on the values of Jeltsch et al. [1996]. For low values of dynamic stress, trees have the highest probability of settlement in their local neighborhoods 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 the combination of seed production and the seed establishment of trees versus that of grasses. Grasses have a much more diffuse seed distribution (and therefore in the model settlement of grasses can also take place if no grass neighbors are present) and lower local settlement chances compared to trees in the no-stress situation. The difference in drought stress sensitivity was based on observations from Texas, which, as mentioned before, show a marked increase in tree density in

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**Table 2. 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>Trees Value</th>
<th>Tree Seedlings Value</th>
<th>Grass Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dynamical stress function k</td>
<td>1.0</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Spatial model</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>
</tr>
<tr>
<td>Minimum death chance</td>
<td>0.01</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Maximum settlement probability</td>
<td>0.75</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>Onset of zero settlement probability</td>
<td>0.1</td>
<td>0.2</td>
<td></td>
</tr>
</tbody>
</table>

Note: For explanation of parameters, see text; all are dimensionless.

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**Figure 2.** Probability 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).
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 occupancy of a cell, whether tree, tree seedling or grass, the corresponding parameters are assigned to that cell. No further spatial interactions are included in the model.

During a model run, each time step corresponds to a growing season whose rainfall parameters $\lambda$ and $\alpha$ are sampled from distributions obtained from historical rainfall data in southern Texas. From these values the dynamic water stress experienced by trees, tree seedlings and grasses is then calculated and from there the chances of death and settlement are computed. In the spatial grid the status of the cells is updated depending on the values of the neighboring cells, and the chances of death and settlement. At the next time step new values of dynamic water stress are calculated, death and settlement chances are computed and cell status updated.

4. Model Testing

The spatial model is analyzed both by its global outcome, the number of trees, tree seedlings and grasses present throughout time, and the spatial patterns it generates. First, the sensitivity to the amount of rainfall is studied. Rainfall is the driving external variable of the model, and thus it is important to test the sensitivity of the model outputs to changes in the structure of the rainfall input. An important outcome of the model is the range of rainfall amounts over which there is stable coexistence of trees and grasses. Savannas present tree grass coexistence over wide ranges of total rainfall amounts [Scholes and Archer, 1997], and it is important that the model can reproduce these wide ranges.

The sensitivity to rainfall is tested by changing the rate of occurrence of rainfall events in the point model (represented by $\lambda$, the chance of a rainfall event per day) from very low to high values. The model is each time run for three thousand years with the selected values of $\lambda$ and $\alpha$, and the numbers of trees and grasses throughout the last 1000 years are studied in detail. Each year represents a different growing season resulting from the same parameters $\lambda$ and $\alpha$. The simulation period is chosen so long in order to avoid errors due to initialization, and to be able to select a long time period over which the model outcome can be evaluated for the different runs.

One of the main characteristics of savanna ecosystems is the high variability in interannual total rainfall amounts, reflected in significant fluctuations in the parameters $\lambda$ and $\alpha$ throughout time. This was incorporated in the model by assuming that the parameters $\lambda$ and $\alpha$ are random variables which change from year to year. In the case of long-term rainfall data of southern Texas, $\lambda$ and $\alpha$ have been shown to be well described by gamma distributions characterized by their corresponding mean and standard deviation [D’Odorico et al., 2000]. In this case, for each year of the simulation random values of $\lambda$ and $\alpha$ are sampled from their respective distributions. To investigate the effects of the year-to-year variation of rainfall on the model outputs, several values of standard deviations of $\lambda$ and $\alpha$ distributions were tested and compared to the case when $\lambda$ and $\alpha$ remain constant throughout time. In this way the sensitivity of tree and grass abundances to differences in the strength of rainfall fluctuations can be analyzed.

After these sensitivity tests, the model was run for 100,000 years at current climate conditions in southern Texas. This period of time is of course artificially long when viewed from a climatological and biological point of view, but is used purely as a test for the stability of the tree-grass coexistence, and for the statistical time series analysis (see below), which need long series of data. The coefficients of variation of $\lambda$ and $\alpha$ 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 Texas weather stations (e.g., see Porporato et al. [2001] for an overview). Both the temporal and spatial characteristics of the model output are then analyzed. The temporal series of the rainfall input and the corresponding vegetation output are studied via their power spectra (using Welch method of spectral estimation [Oppenheim and Schafer, 1989]). The results will be described in the next section of this paper.

In addition to the temporal output of the model the spatial dynamics is especially important because of its potential for linking model output to field measurements. Time series of vegetation development in savanna ecosystems are too short in duration to test thoroughly stochastic models like the one presented here. Therefore the analysis of spatial characteristics open avenues to quantitatively test vegetation models and furthermore study temporal dynamics through their impact on spatial patterns. For doing this, robust spatial behavior should be extracted from a stochastic model as well as particular departures from such robust behavior. The term “robust” is defined here as the typical behavior of the model output under different parameter sets.

The spatial fields of the model are analyzed using two characteristics. First, for a consecutive set of 1500 years the spatial distribution of trees is tested for spatial clustering by applying Ripley’s K function [Ripley, 1976; Haase, 1995; Wiegand et al., 1998]. The goal here is to use a simple and fast test of the statistical nature of the spatial patterns that are generated by the model. Field measurements indicate that both random and strongly clustered distributions of trees may exist in the field and the univariate form of Ripley’s K function allows us to investigate whether the model can represent both situations for prolonged periods of time. Ripley’s K function is applied by selecting from each spatial field an inner plot of 70 by 70 cells. 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 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]

$$\hat{K}(l) = n^{-2}A \sum_{i \neq j} w_{ij}^{-1} I_1(u_{ij})$$

(2)

where $n$ is the number of events (trees) in the analyzed field, $A$ is the area of the field, $I_1$ 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 \( u_{ij} / C^2_0 \leq 1 \) the counter variable \( I_1 \) 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 of trees as in the field being tested [Haase, 1995]. By comparing the maximum and minimum K value of the randomization 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 characterization 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 analyze the probability distribution of cluster sizes, the number of clusters larger than a certain size is plotted versus the cluster size, on a log-log scale. The 8 direct neighbors of a 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 other types of

Figure 3. The mean and standard deviation (bars) of cell coverage of trees (including tree seedlings) and grasses as function of \( \lambda \) (mean value of \( \alpha^{-1} = 1.5 \) cm per event). Computations are for the last 1000 years of a 3000 years simulation. \( CV = \) coefficient of variation. (a) \( CV(\lambda) = 0.000 \) and \( CV(\alpha^{-1}) = 0.00 \). (b) \( CV(\lambda) = 0.025 \) and \( CV(\alpha^{-1}) = 0.05 \). (c) \( CV(\lambda) = 0.050 \) and \( CV(\alpha^{-1}) = 0.10 \). (d) \( CV(\lambda) = 0.075 \) and \( CV(\alpha^{-1}) = 0.15 \). (e) \( CV(\lambda) = 0.100 \) and \( CV(\alpha^{-1}) = 0.20 \).
Figure 3. (continued)
simulated fields: those which have an increment in tree density with respect to the previous time step, 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.

5. Results

5.1. Rainfall Sensitivity

[29] The combined effects of increasing rainfall and year-to-year rainfall variability are shown in Figure 3. When there is no interannual variability in the rainfall parameters, for values of $\lambda > 0.11 \text{ d}^{-1}$ the tree population becomes sustainable and shows a sharp increase from a cover of near zero percent to a cover close to 50%. For $\lambda$ values between 0.115 and 0.12 the tree population shows a small decrease in density. This is caused by the fact that at these $\lambda$ values, trees do not experience major water stress (the value of the dynamic stress is below their threshold), whereas the tree seedlings are still under high stress conditions (see Figure 1). 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 $\lambda$ values 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.

[30] The above effect totally disappears when year-to-year variation is included in the rainfall parameters. In this case trees are absent in the lower range of $\lambda$ values, 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. Notice also that increasing the interannual variability of the rainfall parameters leads to an increase of the grass density as well as a decrease in tree coverage when compared with situations that have the same mean values of $\lambda$ and $\alpha$ but smaller interannual variability.

5.2. Time Series Analysis

[31] Figure 4 shows results from 5,000 years of simulation using rainfall parameters representative of the La Copita Research area in Texas [Archer et al., 1988]. Here $\langle \lambda \rangle = 0.18 \text{ d}^{-1}$ with $\text{CV}(\lambda) = 0.2$, $\langle \alpha^{-1} \rangle = 1.5 \text{ cm per event}$, $\text{CV}(\alpha^{-1}) = 0.3$. 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. It is observed that temporal dynamics of the simulated vegetation displays characteristics fundamentally different from those of the rainfall input. Both trees and grasses show medium term and long-term oscillations which are not present in the generated growing season total rainfall amounts. This can be objectively studied through their corresponding power spectra shown in Figure 5.

[32] As expected the spectrum of the rainfall input is flat over the whole frequency range since the rainfall generated without any temporal correlation structure. This was done in this way in order to be able to attribute any temporal structure in the resulting vegetation evolution to the internal dynamics of the model. Drastically different from the rainfall input the model outputs show considerable structure over all frequencies. Most clearly, the power spectra of the density coverage for 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 at all frequencies when the system is driven by simple white noise.

The spectra of the density coverage for trees and tree seedlings show departures from a power law structure. 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 result from dynamic effects arising from the 5-year interval.

Figure 5. Power spectral density plots of the rainfall input and the corresponding proportional abundance of trees, seedlings, grasses, and bare soil for a simulation of 100,000 years (the rainfall characteristics are the same as in Figure 4).
chosen as seedling lifetime and lack special significance. Notice that the spectrum for trees and tree seedlings together does not show the above behavior, and approaches a power law structure. Simulations with different rainfall parameters show qualitative the same type of results.

5.3. Spatial Pattern Analysis

[34] 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 6; also here the initial 500 years were deleted from the model outcome to remove effects of model initialization. In the upper graph the significant departures from the random distributions are shown for length scales of 2 to 15 cells. 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. Since 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 tends to increase in length scales at periods in which there is an increase in tree density. This results from the fact that tree seedling establishment can only occur in the neighborhood of mature trees. When the seedlings become mature trees, the spatial distribution of these is strongly clustered around the trees whose seeds led to the original establishment.

[35] In Figure 7 two fields are shown, which have the same tree density (~15%) but differ totally in their cluster characteristics (field 1 and field 2 in Figure 6). 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 6, 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.

[36] Figure 8 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 large clusters. The deviation for very large sizes is likely the result of the smaller sample size as well as the finite size effects of the domain which with 10,000 cells is obviously small for clusters beyond a few hundred connected trees. The steepness of the power law for the trees-only analysis is larger 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.

[37] In Figure 9 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 with respect to the previous year is smaller than the number of fields obtained with an increase of trees in time: of the total of 140 fields, 90 fields are “increase” fields, and 50 are “decrease” fields. This implies that most of the time, as can also be seen in Figure 4, trees were increasing in density, and decreases in tree density occurred in relatively short time spans of severe drought. The distribution of the decrease type of fields shows a higher slope than that of the increase fields: the decrease fields having relatively more small clusters, caused by the
spatially uncorrelated tree deaths occurring at the moment
the field is analyzed.

6. Discussion
6.1. Model Behavior and Ecological Reality
[33] Measurements in savanna ecosystems show that tree
grass coexistence occurs over wide ranges of rainfall
amounts [Scholes and Archer, 1997]. The results from
the model regarding the effects of rainfall amounts and
their interannual variability show that with an increasing
year-to-year rainfall variability there is a clear trend of
increasing intervals of tree-grass coexistence. 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. Therefore over a broader range of \( \lambda \) values
grasses are present in significant amounts, especially when
considering the increased standard deviation. At the highest
coefficients of variations (CV) applied in this analysis (CV
of \( \lambda = 0.2 \) and CV of \( \alpha^{-1} = 0.1 \)) there is a stable
coeistence between trees and grasses at a \( \lambda \) interval from
0.144 to about 0.17 events per day (e.g., between 320 mm
and 380 mm of mean rainfall per growing season). Values
of the year-to-year variations in rainfall larger than those
shown in Figure 3 were not considered because the
populations of trees and grasses are then still in transient
behavior after 3000 years, and the random rainfall charac-
teristics have a large effect on the mean value of the last
1000 years.

Figure 7. Spatial structures of fields (a) 1 and (b) 2 of Figure 8 (see text for explanation).
When the model is run with the climate characteristics of La Copita Research Area, Texas, the model shows that dynamical coexistence of trees and grasses occurs. Furthermore, the model output also displays fast temporal dynamics: tree density can increase up to 50% in less than 50 years when the climatical conditions are favorable for tree settlement. These fast dynamics have been documented in the field by Archer et al. [1988]: in 1941 the woody plant coverage in La Copita was 13%, in 1960 (after a severe 10 year drought period) it was 8%, and in 1983 following an abnormally wet decade, it was 36%. The woody plant coverage thus increased almost 30% in about 20 years, although there is no doubt that besides the water fluctuations, grazing and fire control also played an important role.

The results of long-term model run of Figure 4 show that trees undergo prolonged periods of low densities. Therefore in a dryer climate or with a lower tree threshold for the dynamic stress, the trees are likely to die out. Also when the interannual growing season rainfall variance is increased, grasses tend to overcome the trees, which may then die out after several 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]. It is clear that a field-based estimate of tree death chances is essential for a reliable model parameterization.

The model can yield totally different spatial distributions even at the same level of vegetation density and may thus account for prolonged periods of both spatially random tree distributions, and spatially clustered tree distributions (see Figures 6 and 7). Both types of spatial patterns have been documented with field data [Jeltsch et al., 1998]. The above result does not mean that soil heterogeneity, redistribution of surface water or processes like animal dispersion of seeds are not important for the spatial distribution of trees found in the field. It only means that from the point of view of a dynamics driven by hydrologic fluctuations such processes are not absolutely essential for explaining differences in tree distribution, although they may be very important in the complex evolution of real ecosystems. Therefore to investigate whether more complex processes like the ones mentioned above should be incorporated into model formulations, it is not enough to study the presence or absence of spatial vegetation clusters. From a heuristic point of view, without clear evidence for more complex processes playing a determining role in the occurrence of vegetation clusters, the most simple explanation tends to be the most illuminating one regarding the emergence of spatial structures. Another problem in linking vegetation clusters to, for example, islands of fertility, is the question whether islands of fertility are the cause for the presence of vegetation clusters, or whether vegetation clusters cause the islands of fertility.

6.2. Ecological Implications

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 tradeoff exists in colonization, competition and longevity [Tilman, 1994]. Disturbance is a key factor for this tradeoff, 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, and works thereby analogous to
arbitrary scaling factor along the time axis, H is the Hurst
1985]).

where d means equality in probability distribution,
g is the
is the
H is the rescaling factor along the axis of
time, H is the Hurst
coefﬁcient and \( H \) is the rescaling factor along the axis of
density coverage. The power spectrum and H are related by
D = 2H + 1 with 0 < H < 1.

The power law structure of the spectrum indicates that the ecosystem avoids getting locked in any dominant
frequency and displays a wide range of dynamic states with
a well deﬁned structure far from complete disorder (e.g., flat
spectrum) or from too much order (e.g., strong cyclic components).
In many biological systems this is a sign of
healthy dynamics which avoid both extremes of order and
disorder (e.g., heart rate variations [Goldberger et al.,
1985]).

An approximate power law exists in the distribution
of cluster sizes, an indicator of the presence of fractal
structures in spatial vegetation patterns and the possible existence of self-organized criticality in the overall dynam-
type of temporal and spatial patterns observed in savanna ecosystems.

7. Conclusions

The results show that the behavior of the model, despite its simplicity, could be linked to ecological reality: the model resulted in dynamic tree-grass coexistence driven by the annual rainfall and the space-time behavior of the model showed that both random and clustered tree distributions for periods up to 100 years could be simulated. Both these tests are of course only qualitative, and the model assumptions and output should be tested more thoroughly. Especially the power law present in the cluster size distribution gives opportunities for this. Both the temporal and spatial model output display fractal characteristics, which point toward the absence of dominant frequencies, or scales, in the space-time dynamics of water controlled ecosystems driven by hydrologic fluctuations. This in turn suggests that these systems tend to self-organize through the interaction of many different processes operating on a wide range of different timescales.

Appendix A: Soil Water Stress Calculation

To link vegetation processes with the drought plants experience, one needs to account for the intensity, frequency and duration of the periods with water stress, i.e., excursions in soil water content values below a threshold $s^*$ (the water content below which water stress is experienced by the plant). Porporato et al. [2001] derived a measure for the mean total vegetation water stress during a growing season. First, a “static” value for the normalized water stress is defined, according to the function

$$\xi(t) = \frac{s - s(t)}{s^* - s_w}$$

for $s_w \leq s(t) \leq s^*$

where $s$ is relative soil water content, $s_w$ is wilting point and further: $0 \leq \xi(t) \leq 1$, $\xi(t) = 1$ for $s > s^*$ and $\xi(t) = 0$ for $s < s_w$. The exponent $q$ accounts for possible nonlinear effects of water deficit on the plant functions.

The probability density function of $\xi$, denoted as $p(\xi)$ for $s_w < s \leq s^*$ can be written as [Laio et al., 2001a; Porporato et al., 2001]

$$p(\xi) = \frac{C_\xi}{n_\xi} \left[ (1 - \frac{\eta}{n_\xi})^{\gamma(1 - \eta)} \right]^{\gamma - 1} \exp \left( -\gamma\eta \right)$$

where

$$\eta = \frac{E_{\text{max}}}{n Z_r}, \quad n_\xi = \frac{E_w}{n Z_r},$$

$$\chi = \lambda \nu^{-1}, \quad \gamma = n Z_r / \chi$$

$Z_r$ is rooting depth, $n$ is porosity, $E_{\text{max}}$ is average daily transpiration under well watered conditions, $\chi^{-1}$ is the mean depth of rainfall events, $\lambda$ is the rate of storm arrivals, $\Delta$ the interception coefficient and $E_w$ is soil evaporation.

The constant of integration $C_\xi$ in Equation 4 can be deduced by imposing the condition

$$\int_0^1 p(\xi)d\xi = p(s^*) - p(s_w) \quad \text{(A3)}$$

where $P(s^*)$ and $P(s_w)$ are the values of the cumulative probability distribution function of soil moisture calculated respectively at $s = s^*$ and $s = s_w$ [see Laio et al., 2001a].

The mean “static” water stress can then be calculated as:

$$\bar{\xi} = \frac{\int_0^1 p(\xi)d\xi + p(1)}{p(1)} \quad \text{(A4)}$$

The value $\bar{\xi}$ obviously also reflects those periods when $\xi$ is 0 and hence it is not very indicative of the actual vegetation conditions [Porporato et al., 2001]. The mean value of water stress given that the plant is under stress, denoted by $\bar{\xi}$ is more meaningful. To obtain $\bar{\xi}$ only the part of the pdf of $\xi$ above zero needs to be considered:

$$\bar{\xi} = \frac{\bar{\xi}}{P(s^*)} \quad \text{(A5)}$$

This value of static water stress, representing the mean vegetation water stress during an excursion below $s^*$, is then combined with the mean duration and the number of occurrences of such excursions during the growing season, denoted respectively by the variables $T_{s^*}$ and $N_{s^*}$. This measure will be called the “dynamic” water stress value, or mean total dynamic stress, $\bar{\theta}$, defined as

$$\bar{\theta} = \frac{\bar{\xi}}{T_{s^*}} \quad \text{if } \bar{\xi} < kT_{s^*}$$

$$\bar{\theta} = 1 \quad \text{otherwise} \quad \text{(A6)}$$

The analytical form of the dynamic water stress is discussed at length by Porporato et al. [2001]. Here we will only note that the function assumes a linear relationship between the mean time under stress, $T_{s^*}$, and the value of dynamic stress, $\bar{\theta}$, 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 (A6) allows to fix the value of this critical threshold: permanent damage appears when $\bar{\xi}/T_{s^*} > kT_{s^*}$, with $k$ representing an index of plant resistance to water stress. The value of $k$ may also be interpreted as the average static stress a plant can experience without suffering permanent damage, 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 for effects of multiple periods of stress on plant status. The functional dependence of $\bar{\theta}$ on $N_{s^*}$ is discussed at length by Porporato et al. [2001]. For values of $N_{s^*}$ smaller than one, $\bar{\theta}$ should increase with $N_{s^*}$. The value of $\bar{\theta}$ is then always below the value of $\bar{\xi}/T_{s^*}/kT_{s^*}$, which corresponds to the value of $N_{s^*} = 1$. In cases when $N_{s^*} > 1$, $\bar{\theta}$ should also increase with $N_{s^*}$ always being above the values corresponding to $N_{s^*} = 1$. 

Furthermore, the impact of large values of $\bar{X}_t$ should be tempered in order to avoid erroneously high values of $\bar{X}_t$ for cases of very short but frequent stress periods. Other functional forms with similar behavior lead to analogous results.

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I. Rodriguez-Iturbe, Department of Civil and Environmental Engineering and Princeton Environmental Institute, Princeton University, Princeton, N. J. 08544, USA.

M. T. van Wijk, Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, King Buildings, Mayfield Road, Edinburgh EH9 3JU, UK. (mark.van.wijk@ed.ac.uk)