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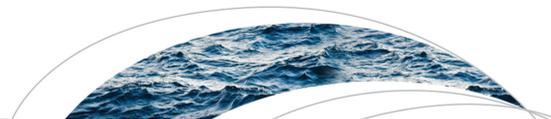
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RESEARCH ARTICLE

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Special Section:

Eco-hydrology of Semiarid Environments: Confronting Mathematical Models with Ecosystem Complexity

Key Points:

- Arid and semiarid savannas are characterized by intermittent rainfall
- Grass coexists with trees and has strong competitive effect on tree seedlings
- The level of rainfall intermittency affects savanna occurrence and structure

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Tree-grass competition for soil water in arid and semiarid savannas: The role of rainfall intermittency

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Abstract Arid and semiarid savannas are characterized by the coexistence of trees and grasses in water limited conditions. As in all dry lands, also in these savannas rainfall is highly intermittent. In this work, we develop and use a simple implicit-space model to conceptually explore how precipitation intermittency influences tree-grass competition and savanna occurrence. The model explicitly includes soil moisture dynamics, and life-stage structure of the trees. Assuming that water availability affects the ability of both plant functional types to colonize new space and that grasses outcompete tree seedlings, the model is able to predict the expected sequence of grassland, savanna, and forest along a range of mean annual rainfall. In addition, rainfall intermittency allows for tree-grass coexistence at lower mean annual rainfall values than for constant precipitation. Comparison with observations indicates that the model, albeit very simple, is able to capture some of the essential dynamical processes of natural savannas. The results suggest that precipitation intermittency affects savanna occurrence and structure, indicating a new point of view for reanalyzing observational data from the literature.

1. Introduction

Savannas occupy about one fifth of the global land surface area, mostly in South America, Africa, and Australia, where grasslands and forests are also observed [Scholes and Archer, 1997; Scholes, 2003]. Savannas are characterized by the coexistence of woody vegetation (i.e., trees and shrubs; called “trees” in the following) and herbaceous vegetation (mainly C4 grasses and herbs; called “grasses” from here on), with varying proportions of these two plant functional forms [Scholes and Walker, 1993; Frost et al., 1986; Ratnam et al., 2011]. Such widespread coexistence has attracted the attention of several ecologists over the last 40 years [e.g., Walter, 1971; Walker and Noy-Meir, 1982; Scholes and Walker, 1993; Scheiter and Higgins, 2007; Sankaran et al., 2005; Hirota et al., 2011; Staver et al., 2011; Murphy and Bowman, 2012]: in many savannas the two life forms often compete for the same resource (mostly water), in apparent contradiction with the prediction of the classical competitive exclusion principle that only one of the competitors can survive [e.g., Hutchinson, 1961].

Savannas receiving less than about 650–1000 mm of rainfall per year on average (i.e., arid and semiarid savannas) [Sankaran et al., 2005] are identified as water limited, since water is the main limit to tree canopy closure, and trees and grasses strongly compete for water. For this type of savannas, other factors, such as fires, grazing, and browsing, can further limit tree presence, but these are not necessary for tree-grass coexistence [Higgins et al., 2007, 2010; Scheiter and Higgins, 2012; Sankaran et al., 2008, 2005; Baudena et al., 2014]. These findings follow from analyses of tree cover data from field sites [Sankaran et al., 2005; Lehmann et al., 2011] and remote sensing [Hirota et al., 2011; Staver et al., 2011], from fire exclusion experiments [Higgins et al., 2007], and from many simple mechanistic models of savanna dynamics [e.g., Scheiter and Higgins, 2007; Accatino et al., 2010; De Michele et al., 2011; Bertram and Dewar, 2013]. In wetter environments (mean annual rainfall above 650–1000 mm yr⁻¹), water availability is high enough for the development of forests. However, savannas are also commonly observed in this range, and fire is considered the key element reducing tree cover and allowing savanna persistence in these more humid environments [e.g., Sankaran et al., 2005; Lehmann et al., 2011; Hirota et al., 2011; Staver et al., 2011, 2012; Accatino and De Michele, 2013; van Langevelde et al., 2003; Hoffmann et al., 2012].

In both humid and dry savannas, trees are recognized to be most vulnerable in their early stages, from seed germination to seedling and sapling growth and survival [e.g., Sankaran et al., 2004; Bond, 2008; February

et al., 2013; Salazar *et al.*, 2012; Wakeling *et al.*, 2011]. Both fires and water limitations can impact tree seedlings heavily [e.g., Salazar *et al.*, 2012; Werner and Prior, 2013], and grasses can strongly limit seedling growth (e.g., via water competition, thermal inhibition, etc.) [Scholes and Archer, 1997; Ball *et al.*, 2002; Riginos and Young, 2007], while these mechanisms are less relevant for deep-rooted, fire resistant, adult trees [Holdo, 2013; Kulmatiski and Beard, 2013; but see also Riginos, 2009]. This so-called tree demographic bottleneck is thus often considered as a key element in explaining tree-grass coexistence [Baudena *et al.*, 2010; Bond, 2008; Sankaran *et al.*, 2004; Staver *et al.*, 2012], analogously to what happens in many other systems of competing consumers, where species coexistence is explained only if life stages are taken into account [de Roos and Persson, 2013].

Here, we will focus on arid and semiarid savannas. As in all other dry lands, rainfall is intermittent and characterized by strong seasonality [e.g., Noy-Meir, 1973]. Plants in these environments are “in general” well adapted to cope with these water pulses [Lundholm and Larson, 2004; Chesson *et al.*, 2004; Rodriguez-Iturbe and Porporato, 2004]. Rainfall occurrence influences vegetation dynamics via soil moisture, in a strongly coupled system where vegetation influences soil water availability as well [e.g., Rodriguez-Iturbe and Porporato, 2004]. Many models have addressed the role of stochastic and intermittent rainfall on the coupled dynamics of vegetation and soil moisture in dry ecosystems [Rodriguez-Iturbe, 2000; Baudena *et al.*, 2007; Baudena and Provenzale, 2008; De Michele *et al.*, 2008; Vezzoli *et al.*, 2008; Scanlon *et al.*, 2005; Siteur *et al.*, 2014]. In particular, in dry lands vegetation survival and persistence are higher when rainfall events are less frequent, for any given value of annual rainfall [Baudena *et al.*, 2007; Kletter *et al.*, 2009]. Most of these studies, however, considered only one type of vegetation, and so far only a few of them have considered the role of precipitation variability on tree-grass coexistence in savannas [e.g., Rodriguez-Iturbe *et al.*, 1999a; Fernandez-Illescas and Rodriguez-Iturbe, 2004; van Wijk and Rodriguez-Iturbe, 2002].

This work aims at investigating theoretically the role of rainfall temporal intermittency in determining the outcome of tree-grass competition, along a precipitation gradient from grassland to savanna, and to forest. We take into account, for the first time to our knowledge, the combined effect of rainfall intermittency and of the changes in tree-grass competition for water during tree life. For this purpose, we introduce a simple ecohydrological model for tree-grass dynamics, representing explicitly water competition and tree demography, which we identify as key elements in arid and semiarid savannas. Following the approach of Baudena *et al.* [2010], we represent separately grasses, tree adults, and seedlings, and we assume that grasses are competitively superior to tree seedlings, but trees can escape this competition once they become adults. The different plant types are represented by a simple implicit-space model for site occupancy, which is based on classical hierarchical competition-colonization models [e.g., Tilman, 1994; Hastings, 1980; Levins, 1969]. Soil moisture dynamics is explicitly represented with a hydrological “bucket” model, representing the water balance in a soil layer as determined by rainfall, hydrological soil properties, and plant water use [Laio *et al.*, 2001; Baudena *et al.*, 2007].

The rest of the paper is organized as follows: In section 2, we introduce the tree-grass-soil moisture model and describe the model calibration. Section 3 reports the results of the simulations, for different precipitation regimes and intermittency levels. Discussion and conclusions are reported in the last section.

2. Methods

2.1. Model Description

We introduced a simple model describing the dynamics of trees and grasses in savannas, including their competition for water, and representing explicitly the tree life stage. The model described the average dynamics of soil and vegetation cover in a large area, using an implicit-space approach. The vegetation was divided into grasses, G , tree seedlings, S , and tree adults, T [following Baudena *et al.*, 2010]. The three life forms were represented by the fraction of space they occupied in a given area, and thus the model represented spatial dynamics implicitly [Tilman, 1994]. Tree, grass, and tree seedling cover was represented by dimensionless variables, varying between 0 and 1, and could not overlap, i.e., $0 \leq T+G+S \leq 1$. The vegetation equations were coupled with an equation for soil moisture s , that is, the average relative soil water content in the root zone throughout the area. Soil moisture dynamics was represented with a simple “bucket” model, originally introduced for water-limited ecosystems [e.g., Laio *et al.*, 2001; Baudena *et al.*, 2007]. The system consisted of the following set of ordinary differential equations:

Table 1. Variables and Functions: Symbols, Meaning, and Physical Dimensions

Symbol	Meaning	Dimension
t	Time	T
G	Grass cover	
S	Tree seedling cover	
T	Adult tree cover	
s	Soil moisture	
$c_G(s)$	Colonization rate for grasses	T^{-1}
$c_T(s)$	Colonization rate for trees	T^{-1}
$r(t)$	Daily rainfall rate	$L T^{-1}$
$l(s, r)$	Infiltration rate of rainfall	$L T^{-1}$
$E_0(s)$	Evaporation rate from bare soil	$L T^{-1}$
$E_G(s)$	Evapotranspiration rate from grasses	$L T^{-1}$
$E_S(s)$	Evapotranspiration rate from tree seedlings	$L T^{-1}$
$E_T(s)$	Evapotranspiration rate from adult trees	$L T^{-1}$
$L(s)$	Leakage	$L T^{-1}$

$$\frac{dG}{dt} = c_G(s)G(1-T-G) - \mu_G G \quad (1)$$

$$\frac{dS}{dt} = c_T(s)T(1-T-G-S) - gS - c_G(s)GS - \mu_S S \quad (2)$$

$$\frac{dT}{dt} = gS - \mu_T T \quad (3)$$

$$\frac{ds}{dt} = \frac{1}{nZ_r} [l(s, r) - (1-T-S-G)E_0(s) - TE_T(s) - SE_S(s) - GE_G(s) - L(s)] \quad (4)$$

The meaning and dimension of the variable and function symbols are listed in Table 1. For the parameter symbols, meaning, and values see Table 2 (based

on Rodriguez-Iturbe and Porporato [2004] and Baudena et al. [2007, 2010, references therein] and based on model calibration, see 2.2).

In this model, the main assumption was that trees were inferior competitors with respect to grasses during the most sensitive stage of their life, i.e., when they were seedlings, but once they grew into adulthood they occupied a space that could not be invaded by grasses [Baudena et al., 2010]. In equation (1), grasses could colonize new areas that were not yet occupied by adult trees or grasses ($1-T-G$), proportionally to their actual coverage (G). They could thus displace tree seedlings, since the space they occupied (S) was considered free for grass colonization. Conversely, tree seedlings, equation (2), could only grow in bare soil ($1-T-G-S$), and their establishment was linearly dependent on the actual adult tree coverage (T). The seedlings grew into adults at rate g (first term on the right-hand side (RHS) of equation (3)), and they could be displaced by grasses proportionally to the grass and tree seedling areas (second and third term, respectively, on the RHS of equation (2)).

Adult trees could not actively displace grasses, so that they were not strictly the best competitor (in the sense of Tilman [1994]), but they could not be out-competed by grasses either, and constituted a spatial limit to their colonization (first term on the RHS of equation (1)). All of the three life forms had extinction rates that were proportional to their actual coverage (with rate μ_G , μ_S , and μ_T for grasses, tree seedlings and adults, respectively). We assumed these mortality rates to be constant, for simplicity, and that $\mu_T < \mu_G < \mu_S$, indicating that adult trees had the lowest mortality, and tree seedlings the highest. We further assumed

Table 2. Parameter Symbols, Meaning, Values, and Measurement Units

Symbol	Meaning	Value	Unit
μ_G	Grass mortality rate	0.5	yr ⁻¹
μ_S	Tree seedling mortality rate	5	yr ⁻¹
μ_T	Adult tree mortality rate	0.02	yr ⁻¹
g	Tree growth rate	0.2	yr ⁻¹
$C_{max,G}$	Grass maximum colonization rate	2	yr ⁻¹
$C_{max,T}$	Tree maximum colonization rate	3	yr ⁻¹
$s_{mc,T}$	Maximum colonization point for trees	0.185	
$s_{mc,G}$	Maximum colonization point for grasses	0.175 (= s^*)	
s_h	Hygroscopic point	0.048	
s_{fc}	Soil field capacity	0.29	
$s_{w,G}$	Wilting point for grasses	0.056	
$s_{w,T}$	Wilting point for adult trees	0.085	
s^*	Fully open-stomata point	0.175	
E_{max}	Maximum evapotranspiration rate	0.38	cm d ⁻¹
E_{fc}	Soil evaporation rate at s_{fc}	0.049	cm d ⁻¹
nZ_r	Soil porosity multiplied by rooting depth	42	cm
K_s	Saturated hydraulic conductivity	20	cm d ⁻¹
β	Water retention parameter	8.5	
N_{wet}	Wet season length	200	d

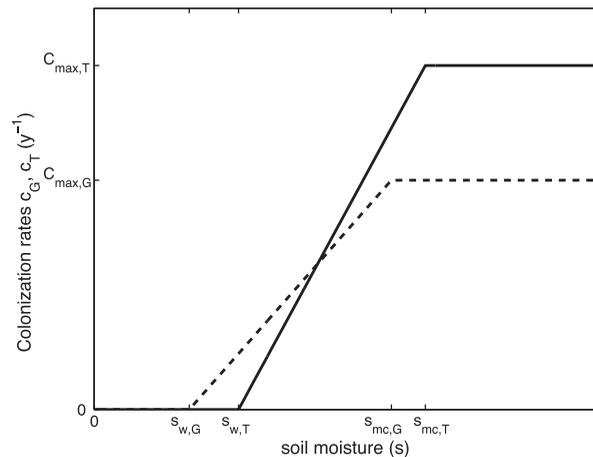


Figure 1. Colonization rates c_G for grasses (dashed line) and c_T for trees (continuous line) as a function of soil moisture s . The values $s_{w,G}$ and $s_{w,T}$ are the wilting points for grass and trees, respectively, whereas $s_{mc,G}$ and $s_{mc,T}$ are the soil moisture values above which grass and tree attain maximum colonization rates. The quantities $C_{max,G}$ and $C_{max,T}$ are the maximum colonization rates for grasses and trees, respectively. These values and the plant water use parameters are reported in Table 2.

and $s_{w,T}$ for trees (defined in connection to the evapotranspiration term, see equation (8)), so that the tree colonization rate depended on the adult tree wilting point. The colonization rates then increased linearly up to a constant value $C_{max,i}$ (different for the two vegetation types), which was reached when soil water was larger than a value $s_{mc,i}$, i.e., the “maximum colonization” point [Baudena and Provenzale, 2008]:

$$c_i(s) = \begin{cases} 0 & \text{if } s \leq s_{w,i} \\ C_{max,i} \frac{(s - s_{w,i})}{(s_{mc,i} - s_{w,i})} & \text{if } s_{w,i} < s \leq s_{mc,i} \\ C_{max,i} & \text{if } s_{mc,i} < s \leq 1 \end{cases} \quad i = T, G \quad (5)$$

For simplicity, we assumed that the maximum colonization point for grasses ($s_{mc,G}$) was equal to the fully open stomata threshold (s^* , defined in connection to the evapotranspiration term in equation (8)) [Laio et al., 2001].

Equation (4) represents the mean water balance in the area of interest, vertically averaged over the root zone, under both bare and vegetated soil (with soil porosity n and root depth Z_r). The quantity $s(t)$ is the relative soil moisture, i.e., the fraction of water per pore soil volume; s is dimensionless, and cannot exceed unity ($0 \leq s \leq 1$). We considered a partial vertical root overlap assuming that grasses and tree seedlings had the same rooting depth ($Z_r = 1$ m) [February and Higgins, 2010], whereas adult trees could also access deeper water [Cipriotti et al., 2014], although we included this only implicitly, when assuming competitive superiority of adult trees. Furthermore, we assumed that within this layer, soil and plant characteristics were homogeneous, thus they could be interpreted as an average over the whole soil layer depth. Note, also, that we represented only the average soil moisture in the whole area described by the model, without making a distinction between soil moisture below trees, seedlings, grasses, and bare soil.

The water input in the soil is the rainfall infiltration rate $I(s, r)$ [Laio et al., 2001], which we assumed to be equal to the daily rainfall rate $r(t)$ if the soil layer was not saturated, whereas, whenever the rainfall amount exceeded the available water storage in the soil, the excess was converted into surface runoff, as:

$$I(s, r) = \begin{cases} r & \text{if } r\Delta t < nZ_r(1-s) \\ nZ_r \frac{(1-s)}{\Delta t} & \text{if } r\Delta t \geq nZ_r(1-s) \end{cases} \quad (6)$$

where $\Delta t = 1$ day. Surface runoff was assumed to leave the area of interest, by direct evaporation or surface river flow.

that the growth rate of seedlings into adult trees (g) was constant, representing the fact that seedlings turn into adults at a certain age.

The colonization rates in equations (1) and (2) combined different processes related to plant settlement into new areas, such as the ability of plants to produce seeds, and the probability of the seeds to germinate and grow into seedlings. In the model, we coupled the equations for vegetation dynamics from Baudena et al. [2010] to soil water availability, inserting a dependence of the colonization rates of herbaceous and woody vegetation (c_G and c_T , respectively) on soil moisture [Sterck et al., 2011] (Figure 1). We assumed that the colonization rate was zero, for both plant types, if soil moisture was lower than the wilting point, $s_{w,G}$ for grasses

To investigate the effect of rainfall intermittency on the tree-grass dynamics, we represented the daily rainfall input $r(t)$ in two different ways: a continuous sequence of rainy days with constant daily rainfall intensity, and a discontinuous sequence of different stochastic events (intermittent rainfall). The latter case was simulated as a Poisson process, with average event occurrence in time λ (d^{-1}). In this case, each rainfall event had a fixed duration of 1 day (but see below for a discussion of the role of event duration) and a given cumulated rainfall amount over the event, which was extracted from an exponential distribution with mean α (mm d^{-1}). These two processes were independent, and we assumed λ and α to be constant [Laio *et al.*, 2001].

We simulated arid and semiarid savannas along a mean annual rainfall (MAR) gradient, considering the range $\text{MAR} = 100 - 1000 \text{ mm yr}^{-1}$ (running simulations every 30 mm yr^{-1}). Since savanna rainfall regimes are highly seasonal, we assumed wet seasons of fixed length $N_{\text{wet}} = 200$ days. We then assumed that vegetation dynamics was “frozen” during the dry season (i.e., all the variables stay constant), and we simulated only the wet seasons, assumed to coincide with the growing season of trees and grasses [Baudena *et al.*, 2007]. This assumption, albeit extreme, does not have significant qualitative effects on vegetation dynamics in such models [Baudena *et al.*, 2007], but future extensions should include explicitly modeling the dynamics during the dry season.

The output terms of the soil water balance (equation (4)) represent three different mechanisms: evaporation from bare soil surface, $(1 - T - S - G)E_0(s)$ (see equation (7)); evapotranspiration from the fraction of soil surface covered by trees, $TE_T(s)$, tree seedlings, $SE_S(s)$, and grasses, $GE_G(s)$ (see equation (8)); and leakage at the lowest boundary of the soil layer, $L(s)$ (see equation (9)).

Evaporation from bare soil (E_0) was described as Baudena *et al.* [2007]:

$$E_0 = \begin{cases} 0 & \text{if } s \leq s_h \\ E_{fc} \frac{s - s_h}{s_{fc} - s_h} & \text{if } s_h < s \leq s_{fc} \\ E_{fc} & \text{if } s_{fc} < s \leq 1 \end{cases} \quad (7)$$

where E_0 was assumed to be zero below the hygroscopic point ($s = s_h$), and then increasing linearly up to a maximum value E_{fc} when soil moisture was equal to the soil field capacity s_{fc} (defined in connection to leakage losses, see equation (9)). In arid and semiarid environments, evaporation from bare soil is confined to the soil surface, around the first 5–20 cm. In this layer, evaporation rate accounts for about half of the total water losses, and can be larger than plant transpiration [Scholes and Walker, 1993; D’Odorico *et al.*, 2005]. In the deeper soil layers, evaporation is very slow, and it contributes negligibly to the soil water balance [Bertram and Dewar, 2013; Baudena and Provenzale, 2008]. To compensate for the fact that we modeled a single soil layer with depth of 1 m, which is much deeper than the layer directly involved in bare soil evaporation, we assumed that the maximum evaporation was much smaller than the maximum evapotranspiration from vegetated soil ($E_{fc} \ll E_{\text{max}}$, defined in equation (8)).

The evapotranspiration terms E_T , E_S , and E_G , from the areas covered by adult trees, tree seedlings, and grasses, respectively, were the sum of plant transpiration and direct evaporation from the soil. Their functional forms, as a function of soil moisture, were assumed to be the same for the three life forms:

$$E_i(s) = \begin{cases} 0 & \text{if } s \leq s_h \\ E_{fc} \frac{s - s_h}{s_{fc} - s_h} & \text{if } s_h < s \leq s_{w,i} \\ E_{w,i} + (E_{\text{max},i} - E_{w,i}) \frac{s - s_{w,i}}{s_i^* - s_{w,i}} & \text{if } s_{w,i} < s \leq s_i^* \\ E_{\text{max},i} & \text{if } s_i^* < s \leq 1 \end{cases} \quad i = T, G, S \quad (8)$$

For a given environment with certain soil characteristics, we assumed that the plant evapotranspiration occurred at a constant maximum rate E_{max} as long as the soil moisture content was large enough for the plants to be fully functional, i.e., $s \geq s^*$. Below the critical value s^* , at which plants start to close their stomata, the evapotranspiration rate was assumed to decrease linearly with s . At the wilting point s_w , plants fully close their stomata; below this critical value only soil evaporation takes place, and we assumed it (in

analogy with equation (7)) to decrease linearly from the value $E_w = E_{fc} \frac{s_w - s_h}{s_{fc} - s_h}$ at s_w to zero at the hygroscopic point s_h [Laio et al., 2001].

For simplicity, we assumed that the fully open-stomata points (s^*) and the maximum evapotranspiration rates E_{max} were the same for both plant types, and that the wilting points of grasses and tree seedlings were equal, thus $s_{w,S} \equiv s_{w,G}$. The exact values of these parameters were not well known in the literature, however, these choices were not crucial for the model results reported in the following. Finally, we assumed that grasses and tree seedlings had a smaller wilting point than adult trees, i.e., $s_{w,G} < s_{w,T}$ [Scholes and Walker, 1993; Rodriguez-Iturbe et al., 1999b].

The leakage losses (L) are the water losses below the rooting zone due to gravity and occur whenever the soil moisture exceeds the soil fields capacity s_{fc} . Below this value, losses from leakage are assumed to be negligible with respect to the evapotranspiration losses [Laio et al., 2001]. We described the leakage term as an increasing exponential function of s , starting at the s_{fc} value and reaching the saturated hydraulic conductivity K_s at $s = 1$, in both vegetated and bare soil:

$$L(s) = K_s \frac{e^{\beta(s-s_{fc})} - 1}{e^{\beta(1-s_{fc})} - 1}, \text{ if } s_{fc} < s \leq 1 \quad (9)$$

where the parameter values are listed in Table 2.

2.2. Model Calibration

The standard sequence of biomes observed for increasing MAR is grassland, savanna, and then forest. A first question was to determine for which parameter values the model was able to reproduce this sequence.

Preliminary investigation of this issue indicated that the functional forms of the colonization rates (see Figure 1) were the essential ingredients for obtaining a correct biome sequence. However, the exact values of the parameters determining such functional forms were not easily measurable or available from the literature, especially for what concerns the maximum colonization rates ($C_{max,T}$ and $C_{max,G}$) and the soil moisture thresholds at which they were attained ($s_{mc,T}$ and $s_{mc,G}$). To overcome this problem, we explored a large set of parameter values, using a Monte Carlo approach, to identify the range of parameters that generated the expected biome sequence. This strategy, which excludes unrealistic parameter combinations, is also known as “pattern-oriented model parameterization” approach [Jakoby et al., 2014; Arnold et al., 2009].

Exploration of variations in the values of $C_{max,T}$, $C_{max,G}$, $s_{mc,T}$, and $s_{mc,G}$ (not shown) indicated that for realistic parameter values the sequence of biomes was qualitatively determined by the relationships between the functional forms of trees and grasses, that is, by the ratios of corresponding parameters in the two forms. To explore the dependence of the model results on these parameters, we thus performed a large number of simulations, each one with a different combination of the values of $C_{max,T}$ and $s_{mc,T}$ while keeping $C_{max,G}$ and $s_{mc,G}$ at the values reported in Table 2.

We randomly generated 10,000 couples of $C_{max,T}$ and $s_{mc,T}$ values in the range $1 \text{ yr}^{-1} \leq C_{max,T} \leq 5 \text{ yr}^{-1}$ and $s_{w,T} \leq s_{mc,T} \leq s_{fc}$ (with $s_{w,T} = 0.085$ and $s_{fc} = 0.29$, see Table 2). For each pair of parameter values, the model was integrated using intermittent precipitation forcing for several different values of mean annual rainfall in the range 100–1000 mm yr⁻¹. For each given value of MAR, we generated precipitation time series with fixed mean daily rainfall intensity ($\alpha = 20 \text{ mm d}^{-1}$) and different expected interarrival time, $N = 1/\lambda$, from 40 days (for 100 mm yr⁻¹) to 4 days (for 1000 mm yr⁻¹). Each simulation (as well as each model run performed in this work) was integrated for a period of 15,000 years, with the same set of initial conditions (with initial nonzero plant cover). The long-term final states of trees ($\bar{T} + \bar{S}$), grasses (\bar{G}), and soil moisture (\bar{s}) were then obtained from the temporal averages over the last 100 years of the simulation, after any possible initial transient decayed away. From the value of these states, we considered the modeled area as vegetated when the average cover of at least one plant type was larger than or equal to $\epsilon = 0.01$, identifying grassland as a state with $\bar{G} \geq \epsilon$ and $(\bar{T} + \bar{S}) < \epsilon$, forest state when $(\bar{T} + \bar{S}) \geq \epsilon$ and $\bar{G} < \epsilon$, and savanna state when both trees and grasses had average cover larger than or equal to ϵ . Interestingly, the long-term final states did not depend on the initial conditions, suggesting that this model system tended to a well defined and unique average state.

The results of the Monte Carlo approach indicated that the expected sequence of grassland, savanna, and forest along the increasing rainfall gradient could be obtained in a large area of parameter space (Figure 2).

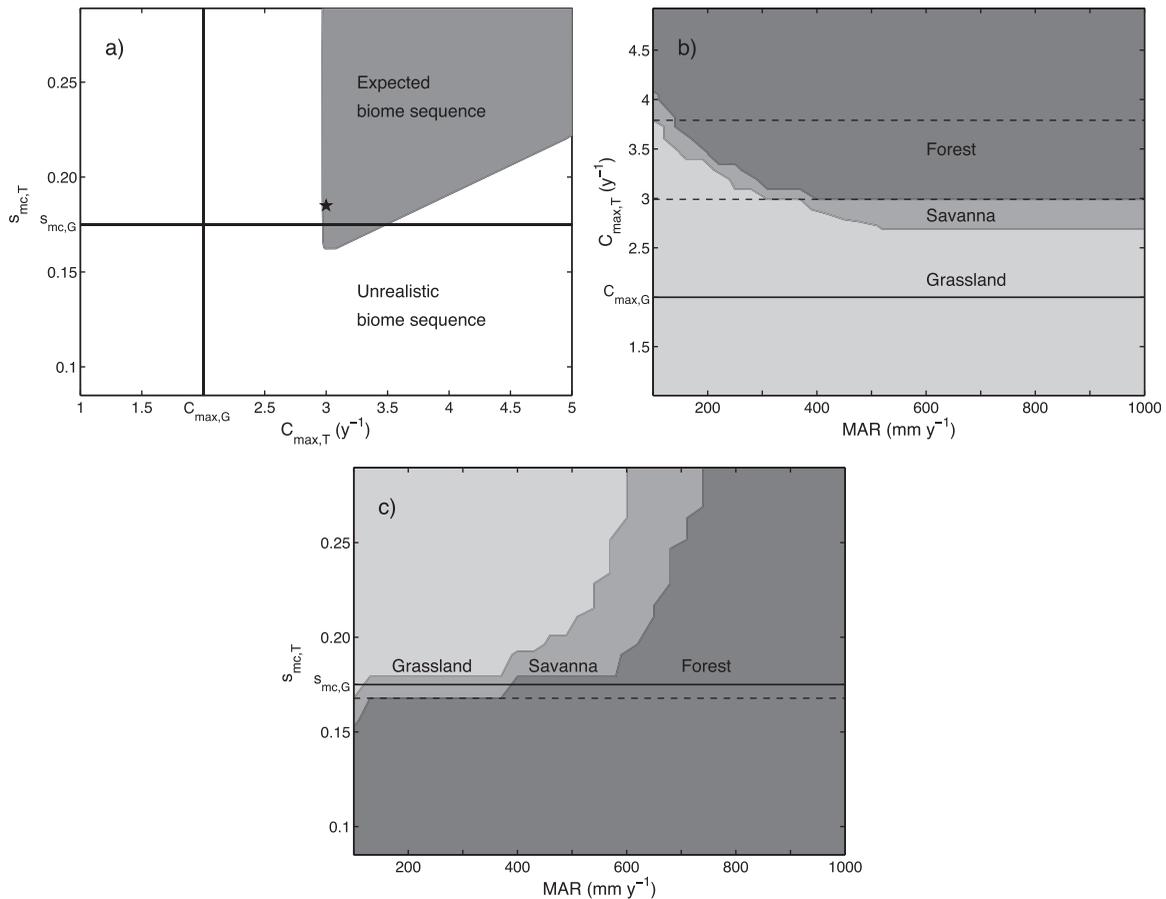


Figure 2. Results of the Monte Carlo simulations performed to identify the areas in the parameter space where the model reproduces the expected biome sequence as a function of mean annual rainfall (MAR). (a) Parameter space of $C_{max,T}$ and $s_{mc,T}$. In the dark gray (white) area, the randomly selected couples of parameters lead (do not lead) to the expected sequence of grassland, savanna, and forest biomes along an increasing MAR gradient. Within the dark gray area, the star symbol represents the couple of $C_{max,T}$ and $s_{mc,T}$ values used for the simulations in the rest of the paper (see also Table 2). (b) Biome types obtained for different values of $C_{max,T}$ and MAR (with $0.183 \leq s_{mc,T} \leq 0.184$). The horizontal dashed lines delimit the areas where the expected biome sequence is obtained. (c) Biome types obtained varying $s_{mc,T}$ and MAR, with $3.00 yr^{-1} \leq C_{max,T} \leq 3.01 yr^{-1}$. In all plots, the vertical and/or horizontal continuous black lines indicate the values of $C_{max,G} = 2 yr^{-1}$ and $s_{mc,G} = 0.175$, which are kept constant in the Monte Carlo simulations. The separations between the different areas in the plots were obtained empirically from the Monte Carlo simulations.

In detail, we observed that, within the parameter ranges considered here, the maximum colonization rate $C_{max,T}$ for trees had to be greater than about $3 yr^{-1}$, thus higher than the maximum colonization rate for grasses, fixed to $C_{max,G} = 2 yr^{-1}$ (Figures 2a and 2b). The value of $s_{mc,T}$ could be both smaller or larger than maximum colonization point for grasses ($s_{mc,G} = 0.175$), although in the vast majority of the cases $s_{mc,T}$ was larger than $s_{mc,G}$ (Figures 2a–2c). Notice that the quantitative values of the boundaries between the modeled grassland, savanna, and forest states for increasing MAR values could vary depending on the choice of parameters in the area of parameter space leading to the expected biome sequence (dark gray area in Figure 2a). However, the qualitative behavior of the model did not change for different parameter choices in this range.

Since the aim of our work was to conceptually study the role of precipitation temporal variability in tree-grass dynamics, in the rest of the paper we analyzed in detail a specific configuration of the model parameters, indicated by the star in Figure 2a.

3. Results

In arid and semiarid regions, precipitation is usually sporadic and it is important to understand whether and how the temporal intermittency of precipitation affects vegetation dynamics. To address this issue, we

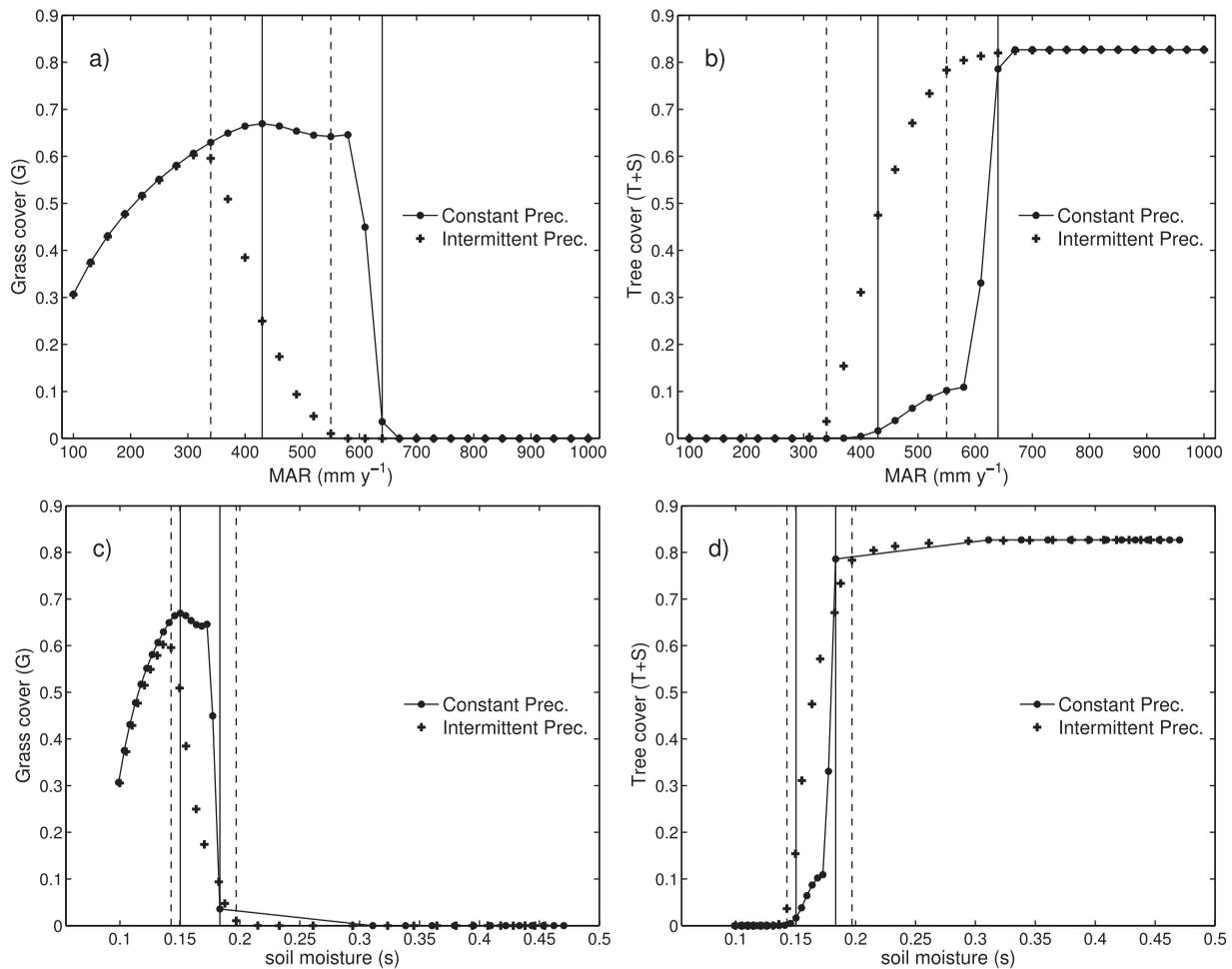


Figure 3. Comparison between (a) grass cover and (b) tree cover obtained with constant (dot-continuous line) and intermittent (cross symbols) precipitation along a mean annual rainfall (MAR) gradient. The two continuous (dashed) vertical lines mark the MAR range 430–640 mm yr⁻¹ (340–550 mm yr⁻¹) for which savanna is found for constant (intermittent) precipitation condition. Plots (c) and (d) show the same as plots (a) and (b), respectively, but as a function of the soil moisture. Vegetation cover and soil moisture values are, for the constant precipitation case, the steady states of the system, whereas for the intermittent case they are the average values after any initial transient has decayed.

compared the situation where the precipitation input was intermittent, along the lines discussed above, with a case where the same annual precipitation was distributed homogeneously over the whole rain season. For each MAR value, we generated intermittent precipitation time series, fixing the mean daily rainfall intensity ($\alpha = 20 \text{ mm d}^{-1}$), and varying the expected interarrival time, as already done in the model calibration phase. Figure 3 shows the vegetation states under constant and intermittent precipitation, for different values of MAR. When rainfall was constant, for each simulated MAR value, soil moisture, and vegetation cover reached a stationary equilibrium. When rainfall was stochastic and intermittent, on the other hand, the system variables fluctuated in time. Thus, we compared the steady state values of vegetation and soil moisture under constant rainfall with their temporal averages in the stochastic case (Figure 3).

At the lower end of the rainfall gradient, the model state was grassland for both constant and intermittent precipitation, and grass cover increased with MAR (Figure 3a). However, the grassland obtained with constant rainfall extended to higher mean annual rainfall values, compared to the intermittent precipitation case. For intermediate MAR values the tree-grass coexistence occurred for both rainfall types. When rainfall was intermittent, for the parameter values chosen here, savanna was obtained for a lower MAR range (about 340–550 mm yr⁻¹) than when precipitation was constant (about 430–640 mm yr⁻¹).

Furthermore, the tree cover in the savanna obtained with intermittent precipitation increased earlier and more steeply than in the case of constant rainfall (see Figure 3b). In the two cases, savanna was observed for ranges of soil moisture that were almost overlapping, with a slightly larger soil moisture range under

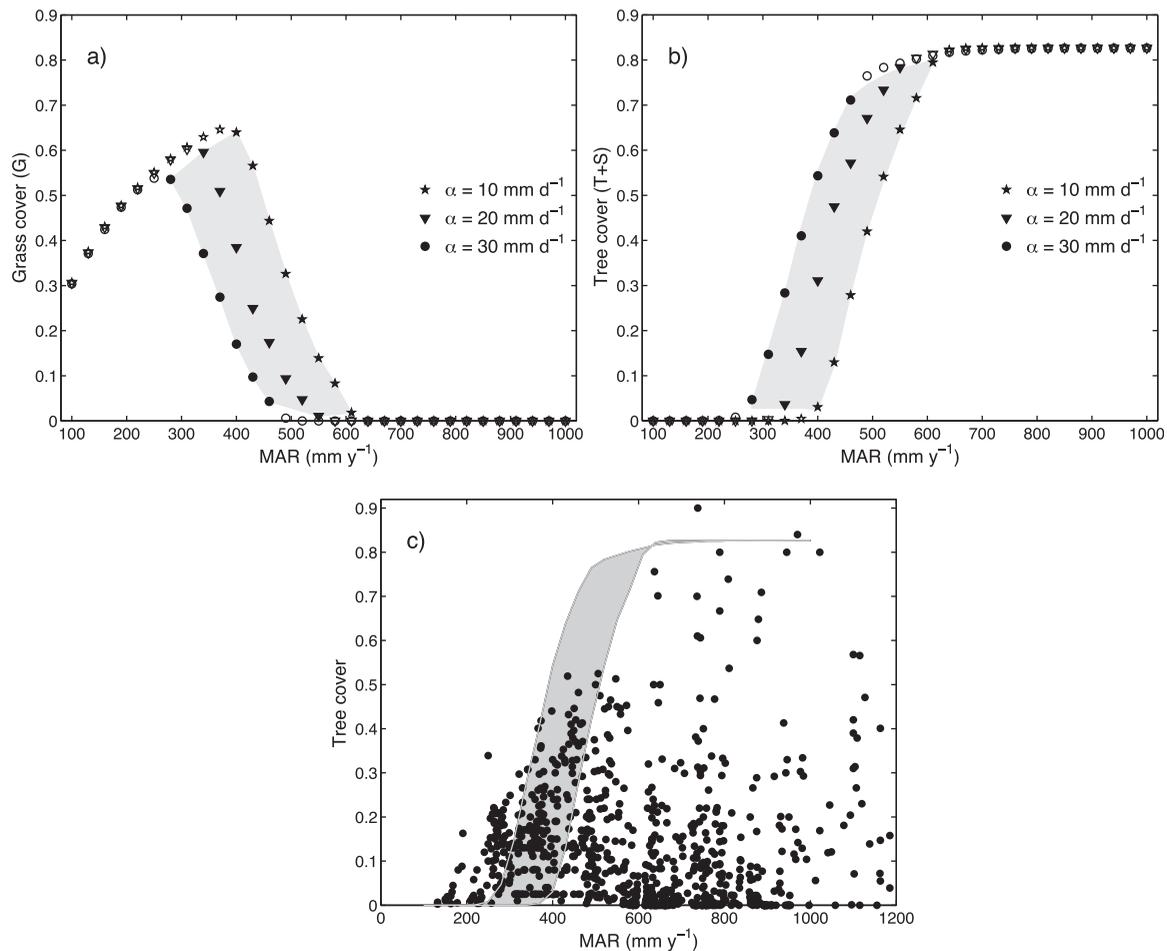


Figure 4. (a and b) Average values of (a) grass cover and (b) tree cover obtained with different levels of precipitation intermittency as a function of mean annual rainfall (MAR). Each symbol corresponds to a different mean intensity of rainfall events, used to generate the precipitation series: stars for $\alpha = 10 \text{ mm d}^{-1}$, triangles for $\alpha = 20 \text{ mm d}^{-1}$ and circles for $\alpha = 30 \text{ mm d}^{-1}$. Empty symbols denote the average (a) grass and (b) tree cover when savanna does not occur, resulting in grassland or forest at low or high MAR, respectively; filled symbols, enclosed in the gray area, indicate (a) grass and (b) tree cover when savannas occur (at intermediate MAR values). (c) Comparison between the observed tree cover variability in African savannas [Sankaran *et al.*, 2005] (black dots), and the average tree cover provided by the model (gray area) for the different levels of precipitation intermittency considered in Figure 4b.

intermittent rainfall conditions (Figures 3c and 3d). Above these ranges, trees formed close forests and excluded grasses, with the forest appearing at lower MAR for intermittent rainfall. Along the increasing MAR gradient, the soil moisture for intermittent rainfall had average values which were similar (low MAR), larger (intermediate MAR), and lower (high MAR) than the constant precipitation values (not shown).

The differences in the model behavior, when forced by intermittent or constant rainfall, were generated by the nonlinearity of the functional forms of the colonization rates and the soil water balance terms [Baudena *et al.*, 2007]. In this model world, precipitation intermittency allowed for tree-grass coexistence at lower levels of water input than those needed for constant rainfall, but in a range of soil water which included the range found with constant precipitation.

We then investigated the effects of different levels of rainfall intermittency on tree-grass dynamics. Thus, we generated different precipitation time series varying the average number and intensity of the rainfall events, varying also MAR along the same gradient as above. We compared the results for three different rainfall regimes, with mean daily rainfall intensity of $\alpha = 10, 20, \text{ and } 30 \text{ mm d}^{-1}$ (Figure 4). At the lower and higher ends of the rainfall gradient, the level of intermittency had little influence on the system behavior, leading to approximately the same average value of grass cover (low MAR) and tree cover (high MAR) for all α values. Tree-grass coexistence occurred at lower MAR when the precipitation occurrence was more sporadic in time, and the individual events were more intense, that is, precipitation was generated with larger

α . In the range of MAR values where savanna occurred for the three values of α , woody vegetation tended to be favored by a higher level of precipitation intermittency (higher N) (see Figure 4b), whereas herbaceous vegetation cover was larger when rainfall events were less intense and more frequent (lower N) (see Figure 4a). For $\alpha = 10 \text{ mm d}^{-1}$, grassland, savanna, and forest occurred for MAR ranges which were similar to those for constant precipitation, but with different proportions of tree and grass covers (see also Figure 3). We finally explored whether the duration of individual rainfall events could play a role, and varied it from 0.5 to 2 days while keeping MAR and N constant (thus changing the daily rainfall intensity from twice to half the value used for a duration of 1 day). This analysis (not shown) indicated that the results were unaffected by varying the event duration in this range.

4. Discussion and Conclusions

In this work we investigated, using a simple ecohydrological model, the effect of different precipitation regimes and intermittency levels on the outcome of tree-grass competition in arid and semiarid savannas. Our model captured the changes in tree-grass water competition with tree life stages. Tree seedlings and grasses have a large rooting overlap in the upper soil layer [e.g., *February and Higgins, 2010; Higgins et al., 2000; House et al., 2003*]. We assumed that grasses outcompete tree seedlings, as a consequence of their superiority in water competition in the same soil layer [e.g., *Kulmatiski and Beard, 2013*], and also for other competitive effects [e.g., *Scholes and Archer, 1997; Ball et al., 2002; Riginos and Young, 2007*]. Once the trees circumvent the demographic bottleneck, adult trees escape grass competition, although they can still affect grasses because they contribute to soil moisture depletion by evapotranspiration, while their growth and mortality are not dependent on soil water availability. The competitive superiority of trees can also be related to the fact that adult trees can often access deeper water [e.g., *Kulmatiski and Beard, 2013*], which can promote tree-grass coexistence especially in arid and semiarid savannas [*Walter, 1971; Ward et al., 2013; Holdo, 2013*].

The model discussed here included the processes discussed above, albeit in a simple way (e.g., excluding other external forcing such as fires), and it predicted the expected sequence of grasslands, savannas, and forests along a gradient of MAR, both with constant and intermittent rainfall. In the model, precipitation intermittency favored tree persistence and disadvantaged grasses, allowing tree-grass coexistence at lower MAR values than in the case of constant precipitation. Furthermore, savanna could be obtained for drier conditions when rainfall intermittency was higher.

In dry lands, precipitation intermittency gives an advantage to vegetation compared to constant precipitation, as episodic intense rainfall events lead to high soil moisture levels, and thus higher values of vegetation colonization rates [*Kletter et al., 2009; Baudena and Provenzale, 2008; Baudena et al., 2007*].

Mathematically, this is a consequence of the Jensen's inequality [*Ruel and Ayres, 1999*]: when a stochastic variable x fluctuates, the average of a nonlinear function $f(x)$ is different from the function of the average of the variable x (i.e., $\overline{f(x)} \neq f(\overline{x})$). In our case, we had a double effect of the nonlinearity of the colonization rate as a function of soil moisture: for intermittent precipitation, the average colonization rates were lower than the colonization rates corresponding to the average soil moisture (i.e., $\overline{c_i(s)} \leq c_i(\overline{s})$, $i = T, G$). However, in the MAR range where savannas were observed, soil moisture was higher for intermittent than for constant rainfall. The combination of these two effects led, in this MAR range, to an average colonization rate for trees which was larger than the values obtained for constant rainfall, while the opposite occurred for grasses. Therefore, in this model intermittent precipitation was beneficial to trees but not to grasses.

For intermittent rainfall, the increase of tree cover with MAR was more gradual than for constant rainfall conditions, in better agreement with the observations that show an upper boundary for tree cover which grows almost linearly with the MAR [*Hirota et al., 2011; Staver et al., 2011; Lehmann et al., 2014; Sankaran et al., 2005*].

Below the maximum value, tree cover observations display a large variability, associated with other factors such as fires and herbivores [*Sankaran et al., 2005; Lehmann et al., 2011*]. Our results suggested that the observed variability of tree cover for arid and semiarid savannas could also be generated by different levels of temporal intermittency in the precipitation (see Figure 4c). Locations with the same MAR across the continents could have different rainfall distributions, as a consequence of different durations of the rainfall season, or of different intermittency levels (e.g., a larger number of small events, or a small number of very

intense events). The duration of the dry season is known to influence savanna because it affects water availability and fire occurrence [Sankaran *et al.*, 2004; Lehmann *et al.*, 2011; Staver *et al.*, 2011; Accatino and De Michele, 2013]. Our results suggested that precipitation seasonality may impact savanna occurrence and structure also as a consequence of different precipitation intermittency during the wet season. However, we did not explicitly simulate savanna dynamics in the dry season, or fire dynamics, and we could not assess the combined effect of all the factors connected to seasonality.

Future projections of global climate models generally indicate a larger probability of intense rainfall events in arid and semiarid regions for the coming decades, even though the projections for annual and seasonal precipitation changes are affected by large uncertainty [Tebaldi *et al.*, 2006; Giorgi *et al.*, 2011]. In view of the results reported here, higher probability of large precipitation events could favor woody encroachment in grasslands and savannas, thus possibly inducing a biome shift in the same direction already expected because of increased CO₂ concentration levels [e.g., Bond and Midgley, 2000; Wigley *et al.*, 2010; Murphy and Bowman, 2012; Baudena *et al.*, 2014].

The simple model introduced here was conceived to study the effect of rainfall intermittence in arid and semiarid savannas on tree-grass coexistence, and could not represent the whole complexity of real savanna dynamics. For example, we chose here not to include fires, which are as important as water limitation in determining savanna existence, and become more and more relevant at higher values of MAR. In particular, we did not obtain bimodality between savanna and forest biomes for large rainfall values, [e.g., Sankaran *et al.*, 2005; Lehmann *et al.*, 2011; Hirota *et al.*, 2011; Staver *et al.*, 2011; Yin *et al.*, 2014], supporting the hypothesis that this bimodality is connected mostly with the existence of a grass-fire feedback [e.g., Higgins *et al.*, 2008; van Langevelde *et al.*, 2003; Staver and Levin, 2012]. Many other factors influence tree-grass coexistence in savannas, such as grazing and browsing [Scheiter and Higgins, 2012; Sankaran *et al.*, 2008], vegetation spatial self-organization [Baudena and Rietkerk, 2012; Nathan *et al.*, 2013], soil edaphic conditions [Lloyd *et al.*, 2008] or facilitative mechanisms [Moustakas *et al.*, 2013; Dohn *et al.*, 2013]. Note, also, that we ignored possible feedback between vegetation and hydrology such as those considered in Baudena *et al.* [2008]. Despite these limitations, our simple model was well suited for studying the potential tree cover (i.e., without fires) in arid and semiarid savannas, which is mainly determined by water competition, while other factors presumably play relatively minor roles [e.g., Murphy and Bowman, 2012]. Our results showed that rainfall intermittency was important for determining savanna occurrence and structure, and suggested a new point of view for reanalyzing observational data on savanna structure.

Acknowledgments

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References

- Accatino, F., and C. De Michele (2013), Humid savanna-forest dynamics: A matrix model with vegetation-fire interactions and seasonality, *Ecol. Modell.*, *265*, 170–179, doi:10.1016/j.ecolmodel.2013.05.022.
- Accatino, F., C. De Michele, R. Vezzoli, D. Donzelli, and R. J. Scholes (2010), Tree-grass co-existence in savanna: Interactions of rain and fire, *J. Theor. Biol.*, *267*(2), 235–242, doi:10.1016/j.jtbi.2010.08.012.
- Arnold, S., S. Attinger, K. Frank, and A. Hildebrandt (2009), Uncertainty in parameterisation and model structure affect simulation results in coupled ecohydrological models, *Hydrol. Earth Syst. Sci.*, *13*(10), 1789–1807, doi:10.5194/hess-13-1789-2009.
- Ball, M. C., J. J. G. Egerton, J. L. Lutz, V. P. Gutschick, and R. B. Cunningham (2002), Mechanisms of competition: Thermal inhibition of tree seedling growth by grass, *Oecologia*, *133*, 120–130.
- Baudena, M., and A. Provenzale (2008), Rainfall intermittency and vegetation feedbacks in drylands, *Hydrol. Earth Syst. Sci.*, *12*(2), 679–689.
- Baudena, M., and M. Rietkerk (2012), Complexity and coexistence in a simple spatial model for arid savanna ecosystems, *Theor. Ecol.*, *6*(2), 131–141, doi:10.1007/s12080-012-0165-1.
- Baudena, M., G. Boni, L. Ferraris, J. Von Hardenberg, and A. Provenzale (2007), Vegetation response to rainfall intermittency in drylands: Results from a simple ecohydrological box model, *Adv. Water Resour.*, *30*(5), 1320–1328.
- Baudena, M., F. D'Andrea, and A. Provenzale (2008), A model for soil-vegetation-atmosphere interactions in water-limited ecosystems, *Water Resour. Res.*, *44*, W12429, doi:10.1029/2008WR007172.
- Baudena, M., F. D'Andrea, and A. Provenzale (2010), An idealized model for tree-grass coexistence in savannas: The role of life stage structure and fire disturbances, *J. Ecol.*, *98*(1), 74–80.
- Baudena, M., et al. (2014), Forests, savannas and grasslands: Bridging the knowledge gap between ecology and dynamic global vegetation models, *Biogeosci. Discuss.*, *11*(6), 9471–9510, doi:10.5194/bgd-11-9471-2014.
- Bertram, J., and R. C. Dewar (2013), Statistical patterns in tropical tree cover explained by the different water demand of individual trees and grasses, *Ecology*, *94*(10), 2138–2144, doi:10.1890/13-0379.1.
- Bond, W. J. (2008), What limits trees in C4 grasslands and savannas?, *Annu. Rev. Ecol. Evol. Syst.*, *39*(1), 641–659, doi:10.1146/annurev.ecolsys.39.110707.173411.
- Bond, W. J., and G. F. Midgley (2000), A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas, *Global Change Biol.*, *6*, 865–869.
- Chesson, P., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin (2004), Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments, *Oecologia*, *141*(2), 236–253.

- Cipriotti, P. A., M. R. Aguiar, T. Wiegand, and J. M. Paruelo (2014), A complex network of interactions controls coexistence and relative abundances in Patagonian grass-shrub steppes, *J. Ecol.*, *102*(3), 776–788, doi:10.1111/1365-2745.12246.
- De Michele, C., R. Vezzoli, H. Pavlopoulos, and R. J. Scholes (2008), A minimal model of soil water-vegetation interactions forced by stochastic rainfall in water-limited ecosystems, *Ecol. Modell.*, *212*(3–4), 397–407, doi:10.1016/j.ecolmodel.2007.10.035.
- De Michele, C., F. Accatino, R. Vezzoli, and R. J. Scholes (2011), Savanna domain in the herbivores-fire parameter space exploiting a tree-grass-soil water dynamic model, *J. Theor. Biol.*, *289*, 74–82, doi:10.1016/j.jtbi.2011.08.014.
- de Roos, A. M., and L. Persson (2013), *Population and Community Ecology of Ontogenetic Development, Monogr. Popul. Biol.*, Princeton Univ. Press, Princeton.
- D'Oudorio, P., F. Laio, and L. Ridolfi (2005), Noise-induced stability in dryland plant ecosystems, *Proc. Natl. Acad. Sci. U. S. A.*, *102*(31), 10,819–10,822.
- Dohn, J., F. Dembélé, M. Karambé, A. Moustakas, K. A. Amévor, and N. P. Hanan (2013), Tree effects on grass growth in savannas: Competition, facilitation and the stress-gradient hypothesis, *J. Ecol.*, *101*, 202–209, doi:10.1111/1365-2745.12010.
- February, E., and S. Higgins (2010), The distribution of tree and grass roots in savannas in relation to soil nitrogen and water, *S. Afr. J. Bot.*, *76*(3), 517–523, doi:10.1016/j.sajb.2010.04.001.
- February, E. C., S. I. Higgins, W. J. Bond, and L. Swemmer (2013), Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses, *Ecology*, *94*(5), 1155–1164.
- Fernandez-Illescas, C. P., and I. Rodriguez-Iturbe (2004), The impact of interannual rainfall variability on the spatial and temporal patterns of vegetation in a water-limited ecosystem, *Adv. Water Resour.*, *27*, 83–95, doi:10.1016/j.advwatres.2003.05.001.
- Frost, P., E. Medina, J. Menaut, O. Solbrig, M. Swift, and B. Walker (1986), Responses of savannas to stress and disturbance, *Biol. Int. Spec. Issue 10*, International Union of Biological Sciences (IUBS), Paris.
- Gorgi, F., E.-S. Im, E. Coppola, N. S. Duffenbaugh, X. J. Gao, L. Mariotti, and Y. Shi (2011), Higher hydroclimatic intensity with global warming, *J. Clim.*, *24*(20), 5309–5324, doi:10.1175/2011JCLI3979.1.
- Hastings, A. (1980), Disturbance, coexistence, history, and competition for space, *Theor. Popul. Biol.*, *18*(3), 363–373, doi:10.1016/0040-5809(80)90059-3.
- Higgins, S., et al. (2007), Effects of four decades of fire manipulation on woody vegetation structure in savanna, *Ecology*, *88*(5), 1119–1125.
- Higgins, S. I., W. J. Bond, and W. S. W. Trollope (2000), Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna, *J. Ecol.*, *88*(2), 213–229.
- Higgins, S. I., W. J. Bond, W. S. W. Trollope, and R. J. Williams (2008), Physically motivated empirical models for the spread and intensity of grass fires, *Int. J. Wildland Fire*, *17*(5), 595–601, doi:10.1071/WF06037.
- Higgins, S. I., S. Scheiter, and M. Sankaran (2010), The stability of African savannas: Insights from the indirect estimation of the parameters of a dynamic model, *Ecology*, *91*(6), 1682–1692.
- Hirota, M., M. Holmgren, E. H. Van Nes, and M. Scheffer (2011), Global resilience of tropical forest and savanna to critical transitions, *Science*, *334*(6053), 232–235, doi:10.1126/science.1210657.
- Hoffmann, W. A., E. L. Geiger, S. G. Gotsch, D. R. Rossatto, L. C. R. Silva, O. L. Lau, M. Haridasan, and A. C. Franco (2012), Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes, *Ecol. Lett.*, *15*(7), 759–68, doi:10.1111/j.1461-0248.2012.01789.x.
- Holdo, R. M. (2013), Revisiting the two-layer hypothesis: Coexistence of alternative functional rooting strategies in savannas, *PLoS One*, *8*(8), e69625, doi:10.1371/journal.pone.0069625.
- House, J., S. Archer, D. Breshears, and R. Scholes (2003), Conundrums in mixed woody-herbaceous plant systems, *J. Biogeogr.*, *30*, 1763–1777.
- Hutchinson, G. E. (1961), The paradox of the plankton, *Am. Nat.*, *95*, 137–145.
- Jakoby, O., V. Grimm, and K. Frank (2014), Pattern-oriented parameterization of general models for ecological application: Towards realistic evaluations of management approaches, *Ecol. Modell.*, *275*, 78–88, doi:10.1016/j.ecolmodel.2013.12.009.
- Kletter, A. Y., J. von Hardenberg, E. Meron, and A. Provenzale (2009), Patterned vegetation and rainfall intermittency, *J. Theor. Biol.*, *256*(4), 574–583, doi:10.1016/j.jtbi.2008.10.020.
- Kulmatiski, A., and K. H. Beard (2013), Root niche partitioning among grasses, saplings, and trees measured using a tracer technique, *Oecologia*, *171*(1), 25–37, doi:10.1007/s00442-012-2390-0.
- Laio, F., A. Porporato, L. Ridolfi, and I. Rodriguez-Iturbe (2001), Plants in water-controlled ecosystems: Active role in hydrologic processes and response to water stress. II: Probabilistic soil moisture dynamics, *Adv. Water Resour.*, *24*(7), 707–723.
- Lehmann, C. E. R., S. A. Archibald, W. A. Hoffmann, and W. J. Bond (2011), Deciphering the distribution of the savanna biome, *New Phytol.*, *191*(1), 197–209, doi:10.1111/j.1469-8137.2011.03689.x.
- Lehmann, C. E. R., et al. (2014), Savanna vegetation-fire-climate relationships differ among continents, *Science*, *343*(6170), 548–552, doi:10.1126/science.1247355.
- Levins, R. (1969), Some demographic and genetic consequences of environmental heterogeneity for biological control, *Bull. Entomol. Soc. Am.*, *15*(3), 237–240.
- Lloyd, J., M. I. Bird, L. Vellen, A. C. Miranda, E. M. Veenendaal, G. Djagbletey, H. S. Miranda, G. Cook, and G. D. Farquhar (2008), Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: A quasi-global estimate, *Tree Physiol.*, *28*(3), 451–68.
- Lundholm, J. T., and D. W. Larson (2004), Experimental separation of resource quantity from temporal variability: Seedling responses to water pulses, *Oecologia*, *141*(2), 346–352.
- Moustakas, A., W. E. Kunin, T. C. Cameron, and M. Sankaran (2013), Facilitation or competition? Tree effects on grass biomass across a precipitation gradient, *PLoS One*, *8*(2), e57025, doi:10.1371/journal.pone.0057025.
- Murphy, B. P., and D. M. Bowman (2012), What controls the distribution of tropical forest and savanna?, *Ecol. Lett.*, *15*(7), 748–758, doi:10.1111/j.1461-0248.2012.01771.x.
- Nathan, J., J. von Hardenberg, and E. Meron (2013), Spatial instabilities untie the exclusion-principle constraint on species coexistence, *J. Theor. Biol.*, *335*, 198–204, doi:10.1016/j.jtbi.2013.06.026.
- Noy-Meir, I. (1973), Desert ecosystems: Environment and producers, *Annu. Rev. Ecol. Syst.*, *4*(1), 25–51, doi:10.1146/annurev.es.04.110173.000325.
- Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins, and M. Sankaran (2011), When is a 'forest' a savanna, and why does it matter?, *Global Ecol. Biogeogr.*, *20*, 653–660, doi:10.1111/j.1466-8238.2010.00634.x.
- Riginos, C. (2009), Grass competition suppresses savanna tree growth across multiple demographic stages, *Ecology*, *90*(2), 335–340, doi:10.1890/08-0462.1.

- Riginos, C., and T. P. Young (2007), Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna, *Oecologia*, *153*, 985–995.
- Rodriguez-Iturbe, I. (2000), Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics, *Water Resour. Res.*, *36*(1), 3–9.
- Rodriguez-Iturbe, I., and A. Porporato (2004), *Ecohydrology of Water-Controlled Ecosystems: Soil Moisture and Plant Dynamics*, Cambridge Univ. Press, Cambridge.
- Rodriguez-Iturbe, I., P. D'Odorico, A. Porporato, and L. Ridolfi (1999a), Tree-grass coexistence in savannas: The role of spatial dynamics and climate fluctuations, *Geophys. Res. Lett.*, *26*(2), 247–250.
- Rodriguez-Iturbe, I., A. Porporato, L. Ridolfi, V. Isham, and D. R. Coxi (1999b), Probabilistic modelling of water balance at a point: The role of climate, soil and vegetation, *Proc. R. Soc. London, Ser. A*, *455*(1990), 3789–3805.
- Ruel, J. J., and M. P. Ayres (1999), Jensen's inequality predicts effects of environmental variation, *Tree*, *14*(9), 361–366.
- Salazar, A., G. Goldstein, A. C. Franco, and F. Miralles-wilhelm (2012), Differential seedling establishment of woody plants along a tree density gradient in Neotropical savannas, *J. Ecol.*, *100*, 1411–1421, doi:10.1111/j.1365-2745.2012.02028.x.
- Sankaran, M., J. Ratnam, and N. P. Hanan (2004), Tree-grass coexistence in savannas revisited—Insights from an examination of assumptions and mechanisms invoked in existing models, *Ecol. Lett.*, *7*(6), 480–490, doi:10.1111/j.1461-0248.2004.00596.x.
- Sankaran, M., N. P. Hanan, and R. J. Scholes (2005), Determinants of woody cover in African savannas, *Nature*, *438*, 846–849.
- Sankaran, M., J. Ratnam, and N. Hanan (2008), Woody cover in African savannas: The role of resources, fire and herbivory, *Global Ecol. Biogeogr.*, *17*(2), 236–245, doi:10.1111/j.1466-8238.2007.00360.x.
- Scanlon, T. M., K. K. Caylor, S. Manfreda, S. A. Levin, and I. Rodriguez-Iturbe (2005), Dynamic response of grass cover to rainfall variability: Implications for the function and persistence of savanna ecosystems, *Adv. Water Resour.*, *28*, 291–302.
- Scheiter, S., and S. I. Higgins (2007), Partitioning of root and shoot competition and the stability of savannas, *Am. Nat.*, *170*, 587–601.
- Scheiter, S., and S. I. Higgins (2012), How many elephants can you fit into a conservation area, *Conserv. Lett.*, *5*(3), 176–185, doi:10.1111/j.1755-263X.2012.00225.x.
- Scholes, R. J. (2003), Convex relationships in ecosystems containing mixtures of trees and grass, *Environ. Resour. Econ.*, *26*, 559–574.
- Scholes, R. J., and S. R. Archer (1997), Tree-grass interactions in savannas, *Annu. Rev. Ecol. Syst.*, *28*, 517–544.
- Scholes, R. J., and B. H. Walker (1993), *An African Savanna: Synthesis of the Nylsvley Study*, Cambridge Univ. Press, Cambridge.
- Siteur, K., M. B. Eppinga, D. Karssenberg, M. Baudena, M. F. Bierkens, and M. Rietkerk (2014), How will increases in rainfall intensity affect semiarid ecosystems?, *Water Resour. Res.*, *50*, 5980–6001, doi:10.1002/2013WR014955.
- Staver, A. C., and S. A. Levin (2012), Integrating theoretical climate and fire effects on savanna and forest systems, *Am. Nat.*, *180*(2), 211–224, doi:10.1086/666648.
- Staver, A. C., S. Archibald, and S. A. Levin (2011), The global extent and determinants of savanna and forest as alternative biome states, *Science*, *334*(6053), 230–232, doi:10.1126/science.1210465.
- Staver, A. C., W. J. Bond, M. D. Cramer, and J. L. Wakeling (2012), Top-down determinants of niche structure and adaptation among African Acacias, *Ecol. Lett.*, *15*(7), 673–679, doi:10.1111/j.1461-0248.2012.01784.x.
- Sterck, F., L. Markesteijn, F. Schieving, and L. Poorter (2011), Functional traits determine trade-offs and niches in a tropical forest community, *Proc. Natl. Acad. Sci. U. S. A.*, *108*(51), 20,627–20,632, doi:10.1073/pnas.1106950108.
- Tebaldi, C., K. Hayhoe, J. M. Arblaster, and G. A. Meehl (2006), Going to the extremes, *Clim. Change*, *79*(3), 185–211.
- Tilman, D. (1994), Competition and biodiversity in spatially structured habitats, *Ecology*, *75*(1), 2–16.
- van Langevelde, F., et al. (2003), Effects of fire and herbivory on the stability of savanna ecosystems, *Ecology*, *84*(2), 337–350, doi:10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2.
- van Wijk, M. T., and I. Rodriguez-Iturbe (2002), Tree-grass competition in space and time: Insights from a simple cellular automata model based on ecohydrological dynamics, *Water Resour. Res.*, *38*(9), 1179, doi:10.1029/2001WR000768.
- Vezzoli, R., C. De Michele, H. Pavlopoulos, and R. J. Scholes (2008), Dryland ecosystems: The coupled stochastic dynamics of soil water and vegetation and the role of rainfall seasonality, *Phys. Rev. E*, *77*(5), 1–9, doi:10.1103/PhysRevE.77.051908.
- Wakeling, J. L., A. C. Staver, and W. J. Bond (2011), Simply the best: The transition of savanna saplings to trees, *Oikos*, *120*, 1448–1451, doi:10.1111/j.1600-0706.2011.19957.x.
- Walker, B. H., and I. Noy-Meir (1982), Aspects of stability and resilience of savanna ecosystems, in *Tropical Savannas*, edited by B. J. Huntley and B. H. Walker, pp. 556–590, Springer, Berlin.
- Walter, H. (1971), *Ecology of Tropical and Subtropical Vegetation*, Oliver and Boyd, Edinburgh, U. K.
- Ward, D., K. Wiegand, and S. Getzin (2013), Walter's two-layer hypothesis revisited: Back to the roots!, *Oecologia*, *172*(3), 617–30, doi:10.1007/s00442-012-2538-y.
- Werner, P., and L. Prior (2013), Demography and growth of subadult savanna trees: Interactions of life history, size, fire season, and grassy understorey, *Ecol. Monogr.*, *83*(1), 67–93.
- Wigley, B. J., W. J. Bond, and M. T. Hoffman (2010), Thicket expansion in a South African savanna under divergent land use: Local vs. global drivers?, *Global Change Biol.*, *16*(3), 964–976, doi:10.1111/j.1365-2486.2009.02030.x.
- Yin, Z., S. C. Dekker, B. J. J. M. van den Hurk, and H. A. Dijkstra (2014), Bimodality of woody cover and biomass in semi-arid regime, *Earth Syst. Dyn. Discuss.*, *5*(1), 83–120, doi:10.5194/esdd-5-83-2014.