An ecohydrological framework for grass displacement by woody plants in savannas

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Abstract During the past several decades, woody plants have been encroaching into grasslands around the world. This transition in plant dominance is often explained as a state shift in bistable ecosystem dynamics induced by fire-vegetation feedbacks. These feedbacks occur when woody plants are able to displace grasses because of their better access to soil water and light. On the other hand, grasses can displace woody plants because of their ability to increase fire frequency and of the higher susceptibility of woody plants to fire-induced mortality. In this study, we present an ecohydrological framework to investigate the displacement of grasses by woody plants. Considering the effect of lateral root spread and of soil water and light limitations, we found that woody plant encroachment can substantially suppress grass production even without the presence of grazers. Bistable dynamics emerge as a result of the grass-fire feedback for a wide range of rainfall conditions, fire susceptibility, and woody plant growth rates.

1. Introduction

The encroachment of woody plants into grasslands has been widely documented in many regions of the world, including the southwestern United States [Archer et al., 1995; Van Auker, 2000], southern Africa [Moleele et al., 2002], Australia [Burrows et al., 1990], Asia [Binggeli, 1996], and the Mediterranean Basin [Maestre et al., 2009]. This phenomenon typically entails either the transition to a savanna state with a mixed community of grasses and woody plants, or—more commonly—the replacement of the grasses with woody plants, often occurring in scattered patches bordered by bare soil [e.g., Schlesinger et al., 1990; Archer et al., 1995]. This change in plant community composition affects the ecohydrological [Huxman et al., 2005] and geochemical [Hibbard et al., 2001] processes, as well as the provision of ecosystem services such as livestock grazing, sheltering of the soil surface, and carbon sequestration.

The transition from grasslands to woodlands has been associated with both exogenic and endogenic factors [D’Odorico et al., 2012]. Exogenic factors are commonly invoked as drivers of the transition and include overgrazing, fire suppression [e.g., Scholes and Archer, 1997], increase in CO₂ concentration [e.g., Morgan et al., 2007; Higgins and Scheiter, 2012], and long-term global changes in rainfall or temperature [e.g., Knapp et al., 2008]. The endogenic factors typically involve positive feedbacks that may create bistable dynamics [D’Odorico et al., 2012]. In other words, it has been argued that the positive feedbacks induce the emergence of two (alternative) stable states associated with grass and woody plant dominance, and that the encroachment of woody plants corresponds to a shift between these two attractors [Anderies et al., 2002; Okin et al., 2009]. This view is supported by the relatively abrupt and irreversible character of woody plant encroachment, as evidenced by the number of unsuccessful attempts to revert woodlands back to the grassland state [Havstad et al., 1999; Rango et al., 2005; Mata-Gonzalez et al., 2007].

One of the major feedbacks arises from interactions between fires and grass biomass. It operates when woody plants have a competitive advantage over grasses in the access to the limiting resource (i.e., soil water) [Van Auker, 2000; Sankaran et al., 2004; D’Odorico et al., 2006; Beckage et al., 2009]. Therefore, in the absence of disturbances the system would tend to complete woody plant dominance. In this feedback, relatively dense grass canopy acting as a continuous stratum of fuel sustains intense fires, thereby killing woody plant seedlings. This positive feedback exists when (a) fire pressure decreases as grass biomass decreases (less grasses → less fires) [e.g., van Wilgen et al., 2000; Lehmann et al., 2011; Staver et al., 2011a, 2011b]; (b) woody plant cover increases with decreasing fire pressure (less fires → more woody plants), as evidenced by fire control experiments [e.g., Bond et al., 2005; Runyan et al., 2012]; (c) grass biomass decreases as woody plant cover increases [e.g., Oba et al., 2000; Eldridge et al., 2011]. While the first two relations have been adequately documented, the ecohydrologic
mechanisms underlying the decrease in grass cover resulting from woody plant encroachment still need to be clarified. There is a general consensus that overgrazing greatly reduces grass biomass and fire frequency, thereby favoring woody plant encroachment [e.g., Anderies et al., 2002; Okin et al., 2009]. However, it remains unclear whether woody plant encroachment itself can reduce grass cover even without the presence of grazers.

In arid and semiarid regions, soil water is the main limiting resource and is therefore considered the determinant of vegetation establishment and growth [Sankaran et al., 2005; Bond, 2008]. Thus, to explain how woody plant cover affects grass production we need to investigate in detail the competitive relations between these two plant functional types with respect to soil water resources. Factors affecting root competition for soil moisture include climate conditions, soil characteristics, and the depth, lateral spread and degree of overlap of plant root systems [Casper and Jackson, 1997; Schenk and Jackson, 2005]. The two-layer model proposed by Walter [1971] postulates that grasses are superior competitors for water in the upper soil layers, while woody plants have exclusive access to water stored in deeper soil layers. The generality of Walter’s hypothesis, however, has been disputed [e.g., Smit and Rethman, 2000; Hipondoka et al., 2003; Sankaran et al., 2004; Beckage et al., 2009]. In contrast to the two-layer model, other studies indicate that tree roots growing in coarse soils can spread laterally rather than vertically [e.g., Schenk and Jackson, 2002; Sternberg et al., 2004]. Through these lateral roots trees can scavenge water from intercanopy areas [Casper et al., 2003; Sternberg et al., 2004; Barbier et al., 2008]. Caylor et al. [2005] proposed a model in which water uptake by the lateral roots can lead to the occurrence of wetter soils under tree canopies than in areas between canopies. However, the extent to which uptake by lateral tree roots can suppress grasses remains poorly quantified.

Another mechanism limiting grass production is associated with woody plant shading, which reduces solar radiation available to grass photosynthesis [Mordue and Menaut, 1995; Lehmann et al., 2011]. This mechanism explains the lower grass biomass found under tree canopies with respect to between-canopy areas [e.g., Moustakas et al., 2013], especially in mesic savannas. In these environments the light limitation resulting from the presence of a relatively dense woody plant canopy limits grass production [e.g., Kim and Eltahir, 2004; Dohn et al., 2013]. In this paper we account for the impact of grass suppression by soil water and light limitations on ecosystem dynamics.

We develop an ecohydrological framework to explain the mechanisms underlying grass displacement by woody plant encroachment. In particular, we evaluate the effect of lateral root spread and canopy shading on soil water and light limitations. By clarifying the relations existing between the fractional cover of woody plants and grass cover, this study sheds light on the processes underlying the grass-fire feedback, a mechanism that is crucial to the emergence of bistable grassland/woodland dynamics.

2. Methods

2.1. Modeling Framework

We develop an ecohydrological framework for the study of the dependence of grass cover on woody plant cover. We investigate the interaction of woody plants and grasses with soil water and light through a coupled energy and water balance model accounting for the competitive advantage of woody plants over grasses. The advantage is enhanced by lateral root spread and woody plant shading. In agreement with other studies [Van Auen, 2000; Sankaran et al., 2004; D’Odorico et al., 2006; Beckage et al., 2009], we assume that woody plants have preferential access to soil water and that in the absence of disturbances (e.g., fires) they would outcompete grasses. This assumption is important in explaining how the rapid shift to a woodland state can be sustained by the grass-fire feedback [Van Auen, 2000; D’Odorico et al., 2006]. We assume that bottleneck effects associated with the higher susceptibility of woody plant seedlings and saplings to fires and drought affects vegetation dynamics only by slowing down the rate of woody plant establishment and growth [Bond, 2008]. Moreover, we assume that fire frequency depends only on grass cover and that all woody plants have the same susceptibility to fire killings. The model couples the surface energy and soil water balance with vegetation dynamics for two plant functional types: woody plants and grasses. It accounts for the grass-fire feedback as a mechanism leading to the possible emergence of bistable dynamics. We parameterize the model using the savannas along the Kalahari Transect in Southern Africa as a case study.

In the model, we consider the surface energy and soil water balance for sites with and without woody plant canopies (hereafter called “under-canopy” and “between-canopy” areas, respectively). Five land cover
components are considered: woody plant canopy, grasses under- and between-woody plant canopies, and bare soil under- and between-woody plant canopies. We denote the woody plant cover as \( f_c \) (\%), and the grass density under and between canopies as \( d_{cg} \) (\%) and \( d_{bg} \) (\%), respectively. Accordingly, the bare soil density under and between canopies can be expressed as \( d_{c} = 1 - d_{cg} \) and \( d_{b} = 1 - d_{bg} \) respectively. The weighted fractions of area covered by grasses and bare soil are:

\[
\begin{align*}
& f_g = (1 - f_c) \times d_{bg} + f_c \times d_{cg} \\
& f_b = (1 - f_c) \times d_{bg} + f_c \times d_{cs} 
\end{align*}

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\[
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& f_g = (1 - f_c) \times d_{bg} + f_c \times d_{cg} \\
& f_b = (1 - f_c) \times d_{bg} + f_c \times d_{cs} 
\end{align*}
\]

The average leaf area index (LAIw, m² m⁻²) of woody land patches is one of the crucial parameters in this model and is related to the average landscape-scale leaf area index through a representation of the landscape as a mosaic of canopy and between-canopy areas resulting from a two-dimensional Poisson distribution of individual woody plants [Caylor et al., 2006]. This representation accounts for vegetation canopy overlapping and provides a framework to calculate LAIw as:

\[
\text{LAIw} = \pi_{wc} \times \text{LAI} 
\]

where \( \pi_{wc} \) is the average number of overlapping woody plant canopies in a woody patch and LAI the leaf area index of an individual woody plant canopy. Each woody plant individual is assumed to have only one canopy. The average number of woody plant canopies in the landscape can be expressed as:

\[
\text{Nc} = n_c \times \pi_{wc} = (1 - f_c) \times \pi_{wc} 
\]

where \( n_c = f_c \times \pi_{wc} \). Following the approach by Caylor et al. [2006], the average number of woody plant canopies in the landscape can be expressed as a function of woody plant cover (\( f_c \)):

\[
\text{Nc} = -\log (1 - f_c) 
\]

Thus, \( -\log (1 - f_c) = f_c \times \pi_{wc} \). Rearranging these equations, the average leaf area index of woody patches can be calculated as:

\[
\text{LAIw} = -\frac{\log (1 - f_c)}{f_c} \times \text{LAI} 
\]

We need to stress that a two-dimensional Poisson distribution assumes no clustering, while savanna trees are often observed in clumps. Because, to date, no close-form solutions exist for clustered two-dimensional stochastic processes of overlapping tree canopies, the Poisson process is here used as a simplified framework for a first-order approximation of the relationship between tree fractional cover and the average number of overlapping canopies in the landscape.

### 2.2. Energy Balance

#### 2.2.1. Shortwave Radiation

The incident shortwave radiation is assumed to vertically irradiate the plant and soil surfaces [Caylor et al., 2005]. Shortwave radiation exponentially decays through the plant canopy (Beer’s law) [e.g., Campbell and Norman, 1998]. Therefore, if \( S_{sky} \) is the average daytime incoming shortwave solar radiation (W m⁻²) above the canopy, the shortwave radiation upon the woody plant canopy (i.e., received by the canopy) is:

\[
S_{dwn} = S_{sky} - S_{dc} = S_{sky} - S_{dcg} - S_{dcs} 
\]

where \( S_{dcg} \) and \( S_{dcs} \) are net shortwave radiations for under-canopy grasses and bare soil respectively. The outgoing longwave radiation of the soil under- and between canopies is:

\[
L_{o} = L_{o,sky} \times \text{E}_{sky}(1 - \text{E}_{sky}) 
\]

\[
S_{sky} = L_{o,sky} + S_{dwn} + S_{dcg} + S_{dcs} 
\]

where \( S_{dcg} \) and \( S_{dcs} \) are net shortwave radiations for under-canopy grasses and bare soil respectively. The outgoing longwave radiation of the soil under- and between canopies is:

\[
L_{o} = L_{o,sky} \times \text{E}_{sky}(1 - \text{E}_{sky}) 
\]

The longwave radiation can be expressed as:

\[
L_{o} = S_{sky} - S_{dc} = S_{sky} - S_{dcg} - S_{dcs} 
\]

#### 2.2.2. Longwave Radiation

Net longwave radiation (\( L_{n} \)) is calculated as the difference between incoming and outgoing longwave radiation. Incoming longwave radiation is given by:

\[
L_{sky} = e_{a} \sigma T^4 
\]

where \( e_{a} \), \( \sigma \), and \( T \) are the thermal emissivity, the Stefan-Boltzmann constant (\( \sigma = 5.670373 \times 10^{-8} \) W m⁻² K⁻⁴), and the atmospheric temperature in Kelvin at reference height (taken to be 10 m), respectively. The thermal emissivity was expressed as:

\[
9.2 \times 10^{-6} T^4 \] [Brutsaert, 1982]. The net longwave radiation of vegetation is assumed to be zero during the daytime [Caylor et al., 2005]. The outgoing longwave radiation of the soil under- and between canopies is expressed as:

\[
L_{o} = (1 - d_{cg}) e_{a} \sigma \text{E}_{c}(1 - \text{E}_{c})^4 + (1 - d_{bg}) e_{a} \sigma \text{E}_{b}(1 - \text{E}_{b})^4 
\]

where \( e_{a} \) is the thermal emissivity of the soil, while \( \text{E}_{c} \) and \( \text{E}_{b} \) are the soil temperatures under and between canopies, respectively. Net longwave radiations for bare soil under and between canopies are then given by:

\[
L_{o} = (1 - d_{bg}) e_{a} \sigma \text{E}_{bg}(1 - \text{E}_{bg})^4 + L_{o}(1 - d_{bg}) L_{o} = L_{o}(1 - d_{bg}) L_{o}(1 - d_{bg}) 
\]

#### 2.2.3. Net Radiation and Available Radiation

Net radiation \( R_{n} \) for each landscape component is:

\[
R_{n} = L_{n} + S_{n} 
\]

Estimations of soil evaporation and transpiration using the Priestley-Taylor approach depend on the quantity of energy available (Q). For the two
soil components, available energy is $Q_v = (1 - C_g) R_n$, where $C_g$ is the ground flux coefficient, which expresses the fraction of $R_n$ contributing to ground heat flux. [Kustas and Norman, 1997; Lhomme and Monteny, 2000]. The latent energy expenditure associated with plant interception ($I_n, \text{mm d}^{-1}$) is $\lambda_v \rho_w \ln$, where $\rho_w$ is the water density ($\text{kg m}^{-3}$) and $\lambda_v$ is the latent heat of vaporization determined as $\lambda_v = 3.1512 \times 10^6 - 2.38 \times 10^3 T_e (\text{J kg}^{-1})$.

2.3. Water Balance

2.3.1. Soil Moisture Dynamics

Our study focuses on the effects of lateral root spread and assumes that grasses and woody plants have the same effective rooting depth ($Z_R$, millimeter). The soil moisture dynamics under and between canopies are expressed through soil water balance equations [Rodriguez-Iturbe et al., 1999; Laio et al., 2001]:

$$n Z_R \frac{d S_c}{d t} = l_c - E_c - L_c,$$

and

$$n Z_R \frac{d S_b}{d t} = l_b - E_b - L_b,$$

where $n$ is the soil porosity, $S_c$ and $S_b$ are the relative soil moisture ($0 < S_c, S_b \leq 1$), $l_c$ and $l_b$ are the infiltration rates, $E_c$ and $E_b$ are the sum of soil evaporation and transpiration, and $L_c$ and $L_b$ are the drainage rates. The subscripts $c$ and $b$ refer to sites under and between canopies, respectively. The mean landscape soil moisture is then calculated as $S = f_c S_c + (1 - f_c) S_b$.

2.3.2. Precipitation

Precipitation ($R$, millimeter) is modeled as a sequence of intermittent rainfall events using a marked Poisson process of storm occurrences with average rainfall frequency, $\lambda$, (events per day). Each storm is modeled as an exponentially distributed random depth with mean, $h$, (millimeter per event) [Rodriguez-Iturbe et al., 1999; Laio et al., 2001].

2.3.3. Interception

The maximum woody plant canopy interception ($I_{n,c,\text{max}}$) and the maximum grass interception ($I_{n,g,\text{max}}$) are both assumed to be constant ($I_{n,c,\text{max}} = 2 \text{ mm}$ and $I_{n,g,\text{max}} = 1 \text{ mm}$) [Scholes and Walker, 1993]. The minimum rainfall depths necessary to generate infiltration under and between canopies are $I_{n,c} = I_{n,c,\text{max}} + d_{cg} \times I_{n,g,\text{max}}$ and $I_{n,b} = d_{bg} \times I_{n,g,\text{max}}$ respectively. Therefore, the interception under and between canopies are given by $I_n = \min(I_{n,c}, R)$ and $I_n = \min(I_{n,b}, R)$, respectively.

2.3.4. Infiltration

Rainfall in excess of $I_n$ and $I_n$ is available for infiltration. Infiltration is limited by the soil storage capacity, which depends on soil depth, porosity, and the current soil moisture. When rainfall is more than $I_n$ and $I_n$, infiltrations under and between canopies are $I_c = \min(R - I_n, n Z_R (1 - S_c))$, $I_b = \min(R - I_n, n Z_R (1 - S_b))$, respectively [Laio et al., 2001].

2.3.5. Transpiration and Soil Evaporation

The rate of potential transpiration and soil evaporation are determined using the Priestley-Taylor equation. Using the Priestley-Taylor equation and excluding the effect of interception, the latent heat flux (LE) is expressed as follows: $LE = \frac{\alpha}{\Delta} Q - \lambda_v \rho_w \ln$, where $Q$ is the energy available for evapotranspiration ($Q = R_n(1 - C_g)$), $\alpha$ is the Priestley-Taylor coefficient, $\gamma$ is the psychrometric constant ($\text{Pa K}^{-1}$), and $\Delta$ is the derivative of the relationship between saturation vapor pressure and air temperature ($\text{Pa K}^{-1}$) [e.g., Campbell and Norman, 1998]. The soil heat fluxes of vegetated surfaces were assumed to be negligible (i.e., $C_g = 0$).

The actual rates of transpiration or soil evaporation are then determined accounting for the dependence on soil moisture availability. To quantify the dependence of transpiration on soil moisture, we follow the approach developed by Rodriguez-Iturbe et al. [1999] and represent the limitation of transpiration by soil moisture as follows:

$$(S) = \begin{cases} 
0, & S < S_{w} \\
S - S_{w}, & S < S' \\
S - S_{w}, & S' < S \\
1, & S \geq S'
\end{cases}$$

where $S$ is the soil moisture, $S'$ is the vegetation-specific value of relative soil moisture above which plants experience unstressed transpiration, and $S_{w}$ is the vegetation-specific wilting point at which point
transpiration ceases. Because woody plants possess lateral roots that expand laterally into between-canopy areas, when determining \( S \), woody plants are assumed to experience the mean landscape soil moisture, \( S \), whereas grasses under and between canopies experience the local soil moisture, \( S_c \) and \( S_b \), respectively. The actual transpiration for each vegetation component is then determined according to the following:

\[
T_{v,e} = \frac{LE_v(S)}{\lambda_v \rho_w},
\]

where \( LE_v \) is the latent heat flux for each vegetation component (i.e., woody plant canopy, grasses under-canopy areas, and grasses between-canopy areas).

Actual soil evaporation also depends on soil moisture. The effect of soil moisture limitation on bare soil evaporation is represented by an exponential function \([Boulet et al., 2000]\),

\[
\beta(S) = \exp[-C_0 k (1/S_w)],
\]

where \( k \) is a (dimensionless) coefficient of limitation. The bare soil evaporation is then expressed as follows:

\[
E_{soil} = \frac{LE_{soil} \beta(S)}{\lambda_v \rho_w},
\]

where \( LE_{soil} \) is the latent heat flux for each bare soil component (i.e., bare soil under-canopy areas and bare soil between-canopy areas).

Woody plant canopy transpiration draws from both the under-canopy and between-canopy soil reservoirs because of lateral root spread, whereas the transpiration of grasses under and between canopies is localized to \( S_c \) and \( S_b \), respectively. The partitioning of the contributions to woody plant canopy transpiration into the under-canopy (PAM\(_c\)) and between-canopy (PAM\(_b\)) soil water stores are expressed as follows:

\[
PAM_c = \begin{cases} 
\frac{S_c - S_{wt}}{(S_c + S_b) - 2S_{wt}} & S_c > S_{wt} \\
0 & S_c \leq S_{wt}
\end{cases}
\]

and

\[
PAM_b = \begin{cases} 
\frac{S_b - S_{wt}}{(S_c + S_b) - 2S_{wt}} & S_b > S_{wt} \\
0 & S_b \leq S_{wt}
\end{cases}
\]

where \( S_{wt} \) is the wilting point of woody plants. To quantify the effects of woody plant cover \( (f_c) \) on between-canopy soil moisture, the portion of woody plant transpiration drawing from the between-canopy soil reservoir is expressed as follows:

\[
T_{sb} = PAM_b T_{(t,c)} \frac{f_c}{1 - f_c},
\]

where \( T_{(t,c)} \) is the woody plant canopy transpiration.

The total transpiration and soil evaporation for the canopy portion of the landscape is \( ET_c = T_{(g,c)} + E_{(s,c)} + PAM_c T_{(t,c)} \), where \( T_{(g,c)} \) and \( E_{(s,c)} \) are the grass transpiration and soil evaporation under-canopy areas, respectively. The total transpiration and soil evaporation for between-canopy areas is expressed as follows:

\[
ET_b = T_{(g,b)} + E_{(s,b)} + PAM_b T_{(t,c)} \frac{f_c}{1 - f_c},
\]

where \( T_{(g,b)} \) and \( E_{(s,b)} \) are the grass transpiration and soil evaporation between-canopy areas, respectively. The total transpiration and soil evaporation for the whole landscape scale is then \( ET = f_c ET_c + (1 - f_c)ET_b \).
2.3.6. Drainage
It is assumed that there is no interaction with underlying soil layers, and consequently, excess soil moisture is expected to drain to field capacity [Caylor et al., 2005]. When soil moisture is larger than field capacity ($S_{fc}$), the drainage under and between canopies are $L_c = nZ_0(S_c - S_{fc})$ and $L_b = nZ_0(S_b - S_{fc})$, respectively.

2.4. Vegetation Dynamics and Equilibrium States
Changes in woody plant cover are modeled as a logistic growth with a mortality term accounting for the effects of fire:

$$\frac{df_c}{dt} = bf_c \left(1 - \frac{f_c}{f_{c\text{max}}} \right) - df_c g(f_g), \quad (1)$$

where $b$ is the woody plant growth coefficient, $f_{c\text{max}}$ the woody plant carrying capacity (i.e., the maximum canopy cover allowed by the limiting resources), $d$ a parameter determining the death rate of woody plants by fires, and $g(f_g)$ a term expressing the control of grass fuel on fire frequency. The relationship between $f_{c\text{max}}$ and mean annual rainfall (MAP) is shown in Figure 1 (based on Sankaran et al. [2005]). The ratio $d/b$ greatly affects the bistable dynamics of woody plants-grass-fire interactions. We assume that $d$ is constant and $b$ increases with the amount of rainfall during the growing season, consistent with other studies [e.g., Dauber et al., 2005; Toledo et al., 2011]. For simplicity, the woody plant growth rate is expressed as a linear function of the growing season rainfall, $R$ (mm): $b = c \times R$, where $c$ (mm$^{-1}$) is a constant. To investigate the sensitivity of the dynamics to changes in the ratio $d/c$, two different values of $d/c$ were considered (Figure 2). Fire frequency is a function of grass biomass. Using data by van Wilgen et al. [2000], we express $g(f_g)$ as follows:

$$g(f_g) = \frac{\eta f_g^2}{1 + (\eta - 1)f_g^2}, \quad (2)$$

where $\eta$ is a coefficient estimated as $\eta = 5$ to match observations (Figure 3) at Kruger National Park (South Africa) by van Wilgen et al. [2000].

Dynamics of grass cover are represented as a logistic growth:

$$\frac{df_g}{dt} = \beta f_g \left(1 - \frac{f_g}{f_{g\text{max}}(f_c)} \right), \quad (3)$$

where $\beta$ and $f_{g\text{max}}(f_c)$ are the grass growth coefficient and the grass carrying capacity, respectively. $f_{g\text{max}}(f_c)$ depends on the woody plant cover.

To quantify the dependence of $f_{g\text{max}}$ on $f_c$, we firstly consider the effect of soil water limitation and then the impact of light limitation. For water limitation, we determine the maximum grass density under ($d_{cgmw}$) and between ($d_{bgmw}$)
canopies corresponding to different values of $f_c$. In other words, because of the initial assumption that canopy cover $f_c$ is independent of grass density (in the absence of fire), we first assign values of $f_c$ and then calculate the maximum grass density that the soil water balance could sustain. To this end, we simulate the soil moisture dynamics for different values of $d_{cg}$ or $d_{bg}$ (depending on whether it is a canopy or between-canopy site) and calculate the average soil moisture. Conditions associated with an average soil moisture during the growing season greater than a critical value—here taken equal to 1.7 times the soil moisture at wilting point of grasses—are considered to be suitable for grass growth. The highest $d_{cg}$ (or $d_{bg}$) corresponding to conditions suitable for grass survival is then the value of $d_{cgm}$ or $d_{bgm}$ corresponding to that value of $f_c$.

To investigate the sensitivity to changes in the critical soil moisture required to sustain maximum grass density, two different values of the wilting point for grasses were considered. To account for light limitation, we determined the maximum density of grasses under and between canopies as $d_{cgm} = l d_{cgm}$ and $d_{bgm} = l d_{bgm}$, respectively, where $l$ is the light limitation coefficient determined as the ratio of actual net photosynthesis rate to saturated net photosynthesis rate (Figure 4), based on leaf-level physiological measurements [O’Halloran, 2007]. $f_{gmax}(f_c)$ is then given by the following:

$$f_{gmax}(f_c) = (1 - f_c) d_{bgm} + f_c \times d_{cgm}.$$  \hspace{1cm} (4)

### 2.4.1. Stable States of the System

The equilibrium states of the ecosystem are obtained by taking the temporal derivatives equal to zero on the left-hand side of equations (1) and (3). Setting the temporal derivative of equation (1) equal to zero and combining equation (1) with equation (2), we obtain the following:

$$f_c = f_{cmax} \left(1 - \frac{d \eta f_g^2}{b (1 + (\eta - 1)f_g^2)} \right).$$  \hspace{1cm} (5)

Likewise, setting the temporal derivative of equation (2) equal to zero and combining equation (2) with equation (4), we obtain the following:

$$f_g = (1 - f_c) d_{bgm} + f_c \times d_{cgm}.$$  \hspace{1cm} (6)

Equilibrium states of the system satisfy both equations (5) and (6) and can therefore be determined as intersections of the corresponding curves in the $(f_c, f_g)$ domain.

### 2.5. Parameterization of the Model

The model is parameterized for the case of savannas along the Kalahari Transect in Southern Africa. This region has a relatively homogenous soil along a south-to-north rainfall gradient and provides an excellent experimental setting to investigate changes in plant community composition associated with different rainfall regimes [Koch et al., 1995]. It has been argued that in the Kalahari environment, variations in temperature are much less

<table>
<thead>
<tr>
<th>Table 1. Location, Elevation (he), Mean Annual Rainfall (MAR), Mean Atmospheric Temperature ($T_{ea}$) in Tshane and Mongu in Southern African</th>
<th>Site</th>
<th>Location</th>
<th>he (m)</th>
<th>MAR (mm)</th>
<th>$T_{ea}$ (K)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tshane</td>
<td>24.164°S, 21.893°E</td>
<td>1118</td>
<td>365</td>
<td>25.3</td>
<td></td>
</tr>
<tr>
<td>Mongu</td>
<td>15.438°S, 23.253°E</td>
<td>1052</td>
<td>879</td>
<td>21.1</td>
<td></td>
</tr>
</tbody>
</table>
important than rainfall in determining vegetation composition and structure [Porporato et al., 2003]. We represent rainfall variability using a Poisson process [e.g., Laio et al., 2001] and use parameters (e.g., rainfall parameters, average daytime incoming solar radiation (S_{sky}), mean atmospheric temperature (T_e), and elevation (h)) from the sites of Tshane and Mongu as representative of semiarid and masic conditions (Table 1) existing along the Kalahari Transect [Scanlon and Albertson, 2004a]. Sensitivity test indicates that model results are insensitive to variations in atmospheric temperature and site elevation. The model operates under the assumption of a statistically homogeneous growing season climate [Laio et al., 2001; Porporato et al., 2003]. The rainy season coincides with the growing season and is assumed to last 210 days from October to May, which accounts for 90% of mean annual rainfall (MAR). The mean of the exponential distribution of the rainstorm depth is taken to be a constant (h = 11 mm d^{-1}), consistent with the finding of a relatively uniform distribution of this parameter across the Kalahari rainfall gradient [Porporato et al., 2003]. In this study, variations in precipitation along the Kalahari rainfall gradient are determined only by changes in the average rainfall frequency (i.e., frequency of rainy days), \(\lambda\). The average daytime incoming solar radiation (S_{sky}) is determined based on energy flux measurements (30 min averages) during the SAFARI 2000 growing season campaign [Scanlon and Albertson, 2004b]. Soil temperature under and between canopies is determined as a function of S_{sky} and air temperature based on two empirical relationships developed by Caylor et al. [2005]: 

\[
\begin{align*}
T_{e,c0} &= \exp(b_1 + b_2 S_{sky} + b_3 T_a) \\
T_{e,c0} &= a_1 + a_2 S_{down} + a_3 T_{e0}
\end{align*}
\]

respectively, where \(a_{1,2,3} \) and \(b_{1,2,3}\) are empirical coefficients, and S_{sky} is expressed as W m^{-2}. The soil water balance equations are integrated numerically with a time step of 0.1 day. The leaf area index of an individual woody plant canopy (LAI) is taken to be 2.5 in our study to match observations from the Kalahari Transect in Southern Africa [e.g., Caylor et al., 2005]. Values of other model parameters are shown in Table 2.

### 3. Results and Discussion

Increases in woody plant cover significantly reduced grass cover in both wet (average rainfall frequency, \(\lambda = 0.4 \text{ d}^{-1}\) and average rainstorm depth, \(h = 11 \text{ mm}\)) and dry (\(\lambda = 0.2 \text{ d}^{-1}\) and \(h = 11 \text{ mm}\)) environments (Figure 5). These results are consistent with experimental observations. For example, Oba et al. [2000] reported that small increases in woody plant cover resulted in marked reductions in grass cover in southern Ethiopia. In a global synthesis of the impacts of woody plant encroachment on ecosystem structure and functioning, Eldridge et al. [2011] found a decrease in grass cover in landscapes affected by woody plant encroachment. The ability of woody plant encroachment to reduce the grass cover is a crucial component of the fire-vegetation feedback commonly invoked to explain the emergence of the grassland/woodland bistable dynamics. Past research argued that the reduction in grass cover could result from exogenous factors such as overgrazing. According to these studies, overgrazing decreases grass cover, thereby reducing fire frequency and thus favoring woody plant encroachment [e.g., Anderies et al., 2002; Okin et al., 2009]. Our
study shows that the reduction in grass cover is likely an effect of woody plant encroachment. The ecohydrological mechanisms underlying this causal relationship are based on the competitive interactions between woody plants and grasses with respect to soil water resources and light. Empirical studies point to the ability of woody plants to exploit soil water resources both under- and between-canopy areas (due to lateral root spread) [e.g., Casper et al., 2003; Caylor et al., 2005; Barbier et al., 2008] and therefore suppress grass production between canopies. Additionally, under-canopy areas light limitation on grass photosynthesis due to woody plant shading further reduces the grass cover, especially in wet environments (where the woody plant canopy is denser) [e.g., Mordelet and Menaut, 1995; Lehmann et al., 2011; Dohn et al., 2013; Moustakas et al., 2013]. We found that in arid environments grass cover is limited mainly by water availability with no major shading effects because the tree cover is relatively low. As tree cover \( f_c \) increases (i.e., in wetter environments), grass growth is predominately limited by light except for the intercanopy patches, which cover an overall small portion of the landscape. Overall the results shown in Figure 5 indicate that woody plant encroachment can markedly reduce grass cover, thereby allowing for the establishment of a positive feedback among grass cover, fire dynamics, and woody plant encroachment [D’Odorico et al., 2012].

We also found that bistable dynamics are characterized by three intersections—between the curves represented by equations (5) and (6)—corresponding to two stable states separated by an unstable one. If the system is in one of the two stable equilibrium points, it will remain in that state unless it is perturbed, while if it is in an intermediate condition, it will converge to one of the two stable states, depending on the initial condition. The grass-fire feedback can lead to the emergence of bistable dynamics both at the dry \( \lambda = 0.2 \, \text{day}^{-1} \) and \( h = 11 \, \text{mm} \) and wet \( \lambda = 0.4 \, \text{day}^{-1} \) and \( h = 11 \, \text{mm} \) sites (Figure 6). If the initial state of the system is a grassland, the system is unable to spontaneously shift to a woodland state because the grassland is a stable configuration (Figure 6). But if a disturbance pushes the system away from the attraction domain of the grassland (i.e., beyond the unstable state in Figure 6), a self-sustained sequence of processes (i.e., grass cover reduction, decrease in fire pressure, and encroachment of woody plants) sustains the shift to the woodland state. Such a shift can be highly irreversible because the state with woody plant dominance is also stable and the system will remain locked therein even after the removal of the disturbance. As noted in section 1, woody plant encroachment is often considered as a state shift in bistable ecosystem dynamics because of the abrupt and apparently irreversible character of this transition, which suggests the existence of internal thresholds and a “fold-type bifurcation” (Figures 6) [D’Odorico et al., 2012].

Precipitation is an important variable that can affect the bistable dynamics of vegetation (Figure 7a). When the mean annual rainfall (MAR) is less than 430 mm \( (\lambda_{\text{MAR}} = 0.06) \), the ecosystem has only one stable state of grassland. In these conditions, woody plants are either not capable of surviving because of water limitations (Figure 1), or because of the relatively high grass biomass, fires are strong enough to kill all the woody plants and prevent the establishment of a tree or shrub canopy. This result is consistent with the observations of grassland dominance in the southern part of the Kalahari transect [e.g., Scholes et al., 2002]. Similar results were obtained by Staver and Levin [2012], although their model allowed for the existence of some woody plants even in dry environments because of the weakening of the fire regime with low grass covers.
Our results show that bistable dynamics associated with grasslands and woodlands occur with the mean annual rainfall (MAR) in the 450–1050 mm range (with $Swg = 0.06$) (Figure 7a). Because of killings by fires sustained by significant grass cover, grasslands remain a stable state of the system; at the same time, because of their ability to suppress grasses, thereby reducing the fire pressure, woodlands are also a stable state of the system. When MAR is greater than 1050 mm, forest (woody plant cover = 100%) and savanna (woody plant cover > 5%) occur as alternative stable states. The existence of savanna as a stable state is due to the decrease in $d/b$ (the ratio between the fire-induced mortality and the growth rate of woody plants) with increasing values of MAR (the rate of post-fire woody plant recovery increases in more humid environments). The emergence of these bistable dynamics is consistent with a number of other studies and experimental observations reported in Table 3. The presence of this bistable regime leads to strong nonlinearities and hysteresis in the ecosystem dynamics with important implications on the ecosystem’s response to "external" drivers such as intense browsing, overgrazing, or increase in CO$_2$ concentration [e.g., Anderies et al., 2002; D’Odorico et al., 2006; Higgins and Scheiter, 2012]. For example, Higgins and Scheiter [2012] indicated that in Africa, an abrupt vegetation shift to woodlands could result from the increase in atmospheric CO$_2$ concentrations. In contrast, intense browsing reduces woody plant cover thereby favoring the grasslands [e.g., Anderies et al., 2002; D’Odorico et al., 2006].

Figure 6. Stable (solid black intersection points) and unstable (white intersection point) states of the dynamics obtained as intersection of curves given by equations (5) (solid line) and (6) (dashed line) in two different rainfall regimes: (a) dry (average rainfall frequency, $\lambda = 0.2$ d$^{-1}$ and average rainstorm depth, $h = 11$ mm) environment and (b) wet ($\lambda = 0.4$ d$^{-1}$ and $h = 11$ mm) environment.
Interestingly, the unstable intersection corresponds to higher values of woody plant cover and tends to become closer to the stable woodland state in wetter environments (Figures 7a and 7b). This occurs because grass production is less limited by water availability despite the presence of woody plant roots spreading laterally into areas between-canopy areas. It is important to stress, however, that—consistent with the experimental findings by Wang et al. [2009]—we have not considered limitations of grass production that in wet environments could result from insufficient availability of nutrients such as nitrogen, phosphorus, and potassium [e.g., Hooper and Johnson, 1999; Van Duren and Pegtel, 2000; Ludwig et al., 2001]. Moreover, we have not considered a possible increase in woodland resilience that could result from the reduction in fire frequency in the more mesic environments [e.g., Cochrane, 2003].

In the presence of fire-vegetation feedbacks, the interplay between woody plant growth and fires determines the bistable ecosystem dynamics [e.g., Hirota et al., 2011; Lehmann et al., 2011; Staver et al., 2011a, 2011b]. Therefore, any factor affecting the rates of woody plant canopy growth and the intensity of fire could affect the bistable regime. As shown in Figure 7a, an increase in the wilting point of grasses extends the bistable range to values of MAR as low as 385 mm, while increasing the resilience of the woodland state. Likewise, a reduction in the d/b ratio enhances the resilience of the woodland state (Figure 7b). While the parameter b (woody plant growth rates) is expected to depend on species interactions, climate, soil characteristics, and disturbances not related to fires [e.g., Holdo, 2006; Coomes and Allen, 2007], woody plant susceptibility to fire (i.e., d) varies with species and growth stage [Bond, 2008].

Figure 7. Stable (solid line) and unstable (dashed line) states as a function of mean annual rainfall (MAR). (a) Wilting point for grass, \( S_{\text{wg}} = 0.065 \) (thick lines) and \( S_{\text{wg}} = 0.06 \) (fine lines) and (b) with different ratios between fire-induced mortality and growth: \( \frac{d}{b} = 750 \) mm (thick lines) and \( \frac{d}{b} = 840 \) mm (fine lines).
Table 3. A Summary of Evidence of the Occurrence of the Fire-Vegetation Feedback (FVF) and Bistability (Bi) (Region MAR (mm) Findings FVF Bi Reference

<table>
<thead>
<tr>
<th>Region</th>
<th>MAR (mm)</th>
<th>Findings</th>
<th>FVF</th>
<th>Bi</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Serengeti (East Africa)</td>
<td>1000</td>
<td>Elephants reduce woody plant cover and fires maintain the stable state of grasslands</td>
<td>Yes</td>
<td>Yes</td>
<td>Dublin et al. [1990]²</td>
</tr>
<tr>
<td>Brazilian Amazon (South America)</td>
<td></td>
<td>Fire has the potential to transform the tropical forest into savannas</td>
<td>Yes</td>
<td></td>
<td>Cochrane et al. [1999]</td>
</tr>
<tr>
<td>Catalonia (Spain)</td>
<td>550</td>
<td>Large tussock grass invasion replaces shrublands because of a fire-grass feedback</td>
<td>Yes</td>
<td></td>
<td>Grigulis et al. [2005]</td>
</tr>
<tr>
<td>Clearing of tropical savannas results in warmer and drier climate, accelerated fire frequencies, and further tree cover loss</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Hoffmann et al. [2002]</td>
<td></td>
</tr>
<tr>
<td>USA and East Africa</td>
<td>500–900</td>
<td>Fires drive and maintain C4 grasslands expansion into woodlands during the late Miocene</td>
<td>Yes</td>
<td></td>
<td>Keeley and Rundel [2005]</td>
</tr>
<tr>
<td>Wet Tropics of Far North</td>
<td>1000–2000</td>
<td>Distinctive features of the vegetation supporting alternative stable states</td>
<td>Yes</td>
<td>Yes</td>
<td>Beckage et al. [2009]²</td>
</tr>
<tr>
<td>Queensland (Australia)</td>
<td></td>
<td>Trees act as engineers that modify fire regimes</td>
<td>Yes</td>
<td></td>
<td>Warman and Moles [2009]²</td>
</tr>
<tr>
<td>Everglades National Park (USA)</td>
<td>1500</td>
<td>The invasive shrubs suppress fire disturbance and convert a savanna to an invasive-dominated forest</td>
<td>Yes</td>
<td>Yes</td>
<td>Stevens and Beckage [2009]²</td>
</tr>
<tr>
<td>Africa, Australia, and</td>
<td>1000–2500</td>
<td>Evidence of forests, savannas, and grasslands as alternative stable states</td>
<td>Yes</td>
<td>Yes</td>
<td>Hirota et al. [2011]²</td>
</tr>
<tr>
<td>South America</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Africa, Australia, and</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>South America</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kruger National Park</td>
<td>600–700</td>
<td>In the absence of fires, the ecosystem becomes a woodland. Fire frequency increases with grass biomass. Increase in CO₂ concentrations induces an abrupt vegetation shift to woodlands</td>
<td>Yes</td>
<td></td>
<td>van Wilgen et al. [2000]²</td>
</tr>
<tr>
<td>(South Africa)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Runyan et al. [2012]²</td>
</tr>
<tr>
<td>Africa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Higgins and Scheiter [2012]</td>
</tr>
<tr>
<td>Emas National Park (Brazil)</td>
<td>1200–2000</td>
<td>Fire-vegetation feedbacks drive and maintain forests and savannas as two stable states</td>
<td>Yes</td>
<td>Yes</td>
<td>Dantas et al. [2013]²</td>
</tr>
</tbody>
</table>

²These references indicate the direct evidence which supports our results of bistability.

In this model we assume that woody plants are better competitors for soil water resources and therefore can outcompete grasses in the absence of disturbances. We need to stress, however, that the competitive dominance of woody plants with respect to grasses changes both with life-history stage and across environmental gradients [Sankaran et al., 2004]. In fact, in some ecosystems grasses are better competitors where they share the same belowground rooting space with woody seedlings and saplings [e.g., Scholes and Archer, 1997; House et al., 2003; Bond, 2008]. Likewise, we do not account for the fact that saplings are more susceptible to fires than adult trees [e.g., Bond, 2008]. In the absence of major bottleneck effects, however, these assumptions are not expected to greatly affect the overall dynamics of grass-woody plant interaction. The higher sensitivity of tree saplings to grass competition and fires is mainly expected to slow-down woody plant growth and enhance woody plant susceptibility to fires.

4. Conclusion

Grass-fire feedbacks are often considered the cause of bistable vegetation dynamics explaining the irreversible transition from a grassland to a woodland state. Crucial to these dynamics is the ability of woody plants to displace grasses in the absence of fires, the ability of fires to decrease woody plant cover, and the ability of grasses to increase fire frequency. This study has elucidated the ecohydrological mechanisms underlying grass displacements by woody plants. It is shown that the displacement is associated with soil water and light limitations which may lead to substantial reductions in grass production following woody plant encroachment. It has also shown that when the ability of woody plants to displace grasses is accounted for, the resulting fire-vegetation feedback induces bistable dynamics for a wide range of rainfall conditions, fire susceptibility, and woody plant growth rates. In these conditions, grasslands become susceptible to (almost) irreversible shifts to the alternative woodland stable state under the action of disturbances.

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Acknowledgments

The authors would like to thank the support from China Scholarship Council. The authors would like to thank the two anonymous reviewers for their constructive and detailed comments on an earlier version of this paper.


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