Grass feedbacks on fire stabilize savannas

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ABSTRACT

Savannas commonly consist of a discontinuous cover of overstory trees and a groundcover of grasses. Savanna models have previously demonstrated that vegetation feedbacks on fire frequency can limit the density of overstory trees, thereby maintaining savannas. Positive feedbacks of either savanna trees alone or trees and grasses together on fire frequency have been shown to result in a stable savanna equilibrium. Grass feedbacks on fire frequency, in contrast, have resulted in stable equilibria in either a grassland or forest state, but not in a savanna. These results, however, were derived from a system of differential equations that assumes that fire occurrence is strictly deterministic and that vegetation losses due to fire are continuous in time. We develop an alternative formulation of the grass-fire feedback model that assumes that fires are discrete and occur stochastically in time to examine the influence of these assumptions on the predicted state of the system. We show that incorporating fire as a discrete event can produce a recurring temporal refuge in which both grass and trees co-occur in a stable, bounded savanna. In our model, tree abundance is limited without invoking demographic bottlenecks in the transition from fire-sensitive to fire-resistant life history stages. An increasing strength of grass feedback on fire results in regular, predictable fires, which suggests that the system can also be modeled using a set of difference equations. We implement this discrete system using modified Leslie/Gower difference equations and demonstrate the existence of a bounded savanna state in this model framework. Our results confirm the potential for grass feedbacks to result in stable savannas, and indicate the importance of modeling fire as a discrete event rather than as a loss rate that is continuous in time.

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1. Introduction

What maintains savanna landscapes as a discontinuous overstory of trees within a graminoid groundcover? Recurring disturbance is one proposed mechanism (House et al., 2003; Sankaran et al., 2004; Gilliam et al., 2006; D'Odorico et al., 2006). In this conceptual model, savannas result from disturbances that depress particular life-cycle stages of trees, limiting tree density and producing an open, unsaturated canopy that facilitates the presence of a graminoid ground cover ('depressant effects hypothesis', e.g., Scholes and Walker, 1993; Higgins et al., 2000; Jeltsch et al., 2000). Fire is a frequent disturbance that functions as a 'depressant effect' in many savanna systems (Bond et al., 2005). Some models of savannas have incorporated fire as a recurrent, but unpredictable and extrinsically determined disturbance that results in non-equilbrial landscapes (e.g., Hoffmann, 1999; Beckage et al., 2006). Other models have considered the fire frequency

in a landscape to result from internal vegetation-fire feedbacks that generate predictable fire regimes and can lead to persistent savannas (e.g., D'Odorico et al., 2006; Beckage et al., 2009). The inclusion of internal feedbacks recognizes that the likelihood of fire is influenced by the composition and abundance of vegetation (e.g., vanWilgen et al., 2003; Mermoz et al., 2005). Some components of savanna vegetation may maintain fire frequency within limits conducive to maintaining the system in a savanna state.

Disturbance models of savannas have been primarily formalized and investigated using differential equations (e.g., van Langevelde et al., 2003; D'Odorico et al., 2006; Beckage et al., 2006; Beckage et al., 2009). This implementation of the underlying conceptual model embodies key simplifying assumptions. One such assumption is that the effect of fire on vegetation is continuous in time, i.e., fire disturbances reduce densities of trees (via reductions in biomass) as rates of loss rather than as events with discrete effects (reductions in densities or biomass of trees). A second assumption is that the occurrence of fire is a strictly deterministic function of biomass without stochasticity (e.g., van Langevelde et al., 2003; Beckage et al., 2006; Beckage et al., 2009). Some model formulations have allowed for stochasticity, but even then only in a limited form (e.g., D'Odorico et al., 2006). These two assumptions likely

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limit the utility of disturbance model predictions for savanna systems.

In this manuscript, we investigate the robustness of savanna disturbance model predictions to the relaxation of these assumptions embodied in previous model formulations. We investigate the influence of formulating fires as discrete and stochastic events on one specific prediction of prior savanna disturbance models: Feedbacks of grass biomass on fire frequency result in either a grassland or forest community but not a savanna with co-occuring trees and grass (D'Odorico et al., 2006; Beckage et al., 2009). We relax the two prior assumptions by allowing fires to be discrete events that are also stochastic in their occurrence in time. We specifically examine the role of grass-fire feedbacks on community dynamics using three modeling approaches: (i) a differential equation model with continuous, deterministic effects of fire, (ii) a differential equation model with discrete, stochastic fire events, and (iii) a difference equation with implicitly discrete fire effects. We examine the role of grass-fire feedbacks on the predicted dynamics of this system using these three modeling frameworks. Approaches (ii) and (iii) relax assumptions inherent in approach (i) by allowing fire to be discrete (ii, iii) and also stochastic (ii). We evaluate the potential for grass feedbacks on fire frequency to result in stable, equilibrial savanna communities containing both trees and grasses.

2. Model description

We explore alternative model formulations using a two-state savanna system with grass and trees. We use the system of differential equations introduced by Beckage et al. (2009) as the basis for our current study. This system of equations utilizes a three-state representation of savannas that includes forest trees, savanna trees, and grasses. We simplify this representation to include only savanna trees and grasses, as is done in many savanna studies (e.g., van Langevelde et al., 2003; Beckage et al., 2006; D'Odorico et al., 2006). Our first representation of savanna dynamics is based on the Lotka–Volterra model of species competition (e.g., Kot, 2001) with one differential equation used to represent the state of each component of the savanna system (trees and grasses).

We explore the effects of a grass-fire feedback on the dynamics of the two-state savanna system. Graminoids dominate the herbaceous groundcover of savannas (Werner, 1991), providing a matrix of well-aerated, flammable fine fuels that are conducive to fire spread. The strength of the grass-fire feedback should depend on the biomass, as well as the pyrogenicity, of grasses (e.g., Brown et al., 2005; Gagnon et al., 2010). We assume that fire frequency will be positively related to the biomass of graminoids—as fine fuels accumulate in the landscape, the likelihood of fire spread across that landscape increases (Higgins et al., 2000; Platt and Gottschalk, 2001). In addition, we incorporate a minimum time for the accumulation of sufficient fuels for a subsequent fire to spread across a landscape, imposing an upper limit on fire frequency of one year (cf. Glitzenstein et al., 2003).

We describe three formulations of a disturbance model of savannas with a feedback of grass biomass on fire frequency.

2.1. Two-state differential equation model

We first represent the dynamics of the savanna system with a system of two differential equations. Our two-state savanna model contains state variables representing tree and grass components in a unit area. The first equation describes the dynamics of tree biomass:

$$\frac{dW}{dt} = r_w W \left(1 - \frac{W}{K_w}\right) - c \left(\frac{G}{K_g}\right) M_w W \tag{1}$$

The left side of (1) represents the instantaneous rate of change of tree biomass W (biomass/area). The right side of Eq. (1) consists of a growth term where the change in tree biomass is described by r_w, which is the intrinsic rate of increase in tree biomass (1/time), and K_w (mass/area), which is the maximum amount of tree biomass that can be supported on a given site (e.g., the carrying capacity). The second term on the right side of Eq. (1) describes the loss of tree biomass resulting from fire. M_w is a constant that represents the proportionate biomass loss rate in fire for trees (1/time). Some authors have argued that fire may not significantly reduce woody biomass in savanna systems because early life history stages are disproportionately affected by fire yet contain little woody biomass (Hanan et al., 2008). Nonetheless, recurrent fires do reduce tree biomass, and we suggest that even low rates can be accommodated in the current model structure, while acknowledging that consideration of different life history stages of trees or living and dead components of biomass could be useful expansions of the model (e.g., Baudena et al., 2010). The term $c(G/K_g)$ represents the frequency of fire: c is a dimensionless parameter that describes the strength of the vegetation feedback on fire, which in this case is driven by grass biomass G (g/m^2) of a given pyrogenicity. K_g is the carrying capacity (mass/area) of the grass layer. Fire frequency is assumed to increase linearly with grass biomass and is bounded between 0 and 1, where 0 corresponds to the absence of fire and 1 represents annual fires. We note that the inclusion of the carrying capacity, K_g, in the feedback term was for convenience; as this term only results in a linear rescaling, the general behavior of the model is not sensitive to the inclusion of this term.

The second equation describes the dynamics of grass biomass:

$$\frac{dG}{dt} = r_g G \left(1 - \frac{G}{K_g} - \frac{W}{K_w}\right) - c \left(\frac{G}{K_g}\right) M_g G \tag{2}$$

The left side of (2) represents the instantaneous rate of change in grass biomass, while the right side contains terms for the growth and loss of grass biomass. Increases in grass biomass are inhibited by the accumulation of grass biomass, just as tree biomass inhibits tree growth in Eq. (1). Growth in grass biomass is also assumed to be reduced by increases in tree biomass, representing the asymmetric competition between the overstory and groundlayer; trees shade ground layer vegetation but the ground layer tends to exert comparatively little effect on the tree layer. This assumption is supported by studies demonstrating that the competitive effect of grasses is not strong enough to prevent rapid recruitment of trees into savannas when fire is excluded (Scholes and Archer, 1997; Higgins et al., 2000; Gilliam et al., 2006).

We simplified the analysis of this two state system by first non-dimensionalizing the equations, reducing the number of parameters prior to investigating their behavior (Kot, 2001). We made the following three substitutions into Eqs. (1) and (2): $T = t r_g$, $g = G/K_G$, and $w = W/K_W$ to arrive at the following simplified system of equations:

$$\frac{dw}{dT} = B_1 w (1 - w) - A_2 g w \tag{3}$$

$$\frac{dg}{dT} = g(1 - g - w) - A_1 g g \tag{4}$$

where $A_1 = cM_G/r_G$, $A_2 = cM_W/r_G$, and $B_1 = r_W/r_G$. The left sides of (3) and (4) now represent the rescaled rates of change of grasses and trees with the state variables g and w varying on the range (0,1). This rescaling reduces the number of model parameters, simplifying the analysis. All terms in the rescaled Eqs. (3) and (4) are now dimensionless. We present results from the simplified system or from the untransformed scale as appropriate.

We analyzed the system of equations to determine the location and stability of equilibrium solutions in which both grass and pines
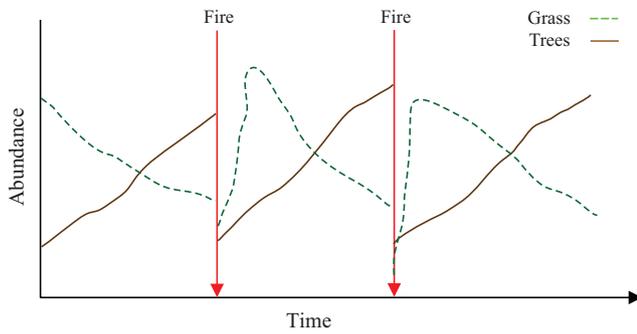
Fig. 1. Illustration of changes in grass and tree biomass in a savanna when fires are discrete events. Each fire results in a reduction of biomass of both the tree and grass components of the savanna, followed by recovery of these components, and resumption of the process of competitive exclusion.

coexist, which is our definition of a savanna. The local stability of an equilibrium indicates whether the system will tend to return to that equilibrium if the system is perturbed or continue to move further away. The equilibria of the dimensional two-state system, for instance, are found by setting $dG/dt = 0$ and $dW/dt = 0$ and then solving for both state variables. The local stability of the equilibria is determined by computing the eigenvalues of the Jacobian, which is given by:

$$J = \begin{bmatrix} \dfrac{\partial\left(\dfrac{dG}{dt}\right)}{\partial G} & \dfrac{\partial\left(\dfrac{dG}{dt}\right)}{\partial W} \\ \dfrac{\partial\left(\dfrac{dW}{dt}\right)}{\partial G} & \dfrac{\partial\left(\dfrac{dW}{dt}\right)}{\partial W} \end{bmatrix}$$

The Jacobian is evaluated at each of the j equilibrium points (G^j, W^j) (Kot, 2001). The eigenvalues were calculated by solving the characteristic equation corresponding to $Det(J_i^* - \lambda I) = 0$ where J_j^* is the Jacobian evaluated at equilibrium point j. The resulting eigenvalues indicate the stability of the corresponding equilibrium. An equilibrium solution is stable when the real component of both eigenvalues is <0, unstable if the real component of either eigenvalue is >0, and the stability is ambiguous if one eigenvalue has negative real part while another has a 0 real part. In the later case, we examined the phase plane to ascertain stability of the equilibrium. Purely imaginary eigenvalues indicate neutrally stable equilibria.

2.2. Differential equation model with discrete, stochastic fire events

We discretized fire events by allowing fires to occur stochastically in discrete time periods of one year in length. We choose one year as the minimum return period for fire (i.e., the time needed for sufficient regrowth of grass biomass to allow fires to burn across the landscape; Johnson et al., 1990; Glitzenstein et al., 2003), recognizing that fire return periods are usually greater than one year. Fires are assumed to reduce biomass of trees and grasses instantaneously, and then both of these savanna components regrow in the time intervals between fires (Fig. 1). Our modified savanna model can be represented by two non-dimensionalized state equations:

$$\frac{dw}{dT} = B_1 w(1-w) - \delta(f)M_w w \tag{5}$$

$$\frac{dg}{dT} = g(1-g-w) - \delta(f)M_g g \tag{6}$$

where the left side and the first term on the right side of (5) and (6) are equivalent to (4) and (5) above. The second term on the right

side of both (5) and (6), however, now represents the potential for fire that results in a discrete loss of biomass in each year. The delta function

$$\delta(f) = 1 \quad \text{if} \ \ f = 1; 0 \ \ \text{otherwise}$$

$$f \sim \text{Bernoulli}(p)$$

$$p = \int_0^g \text{Uniform}(x; ll, ul)dx$$

where ll represents the lower limit of the uniform distribution for g (=0) and ul represents the upper limit (=1). The result is that the probability of fire is linearly related to g just as in Eqs. (3) and (4). We examined the dynamics of the differential equation model by numerically iterating the equations given parameter values and initial conditions.

2.3. Difference equation model

We also investigated a completely discretized version of (3) and (4) based on a modification of the Leslie/Gower difference equation competition model (Cushing et al., 2004). The Leslie/Gower difference equation is an analog to the Lotka–Volterra competition model in the sense that it results in the same set of potential outcomes (Cushing et al., 2004). We modified the Leslie/Gower model to represent the asymmetric competition between grasses and trees in our conceptual model and to include a loss term corresponding to fire disturbance. The dynamics of the system are thus given by:

$$w_{t+1} = \frac{\lambda_w(1-M_w)w_t}{1+(1-M_w)w_t} \tag{7}$$

$$g_{t+1} = \frac{\lambda_g(1-M_g)g_t}{1+c(1-M_w)w_t+(1-M_g)g_t} \tag{8}$$

We identify the equilibria for this system of equations and checked their stability using a procedure analogous to that outlined for the differential equation model above except that eigenvalues between −1 and 1 indicate local stability. We also examined the dynamics of the difference model by iterating the equations given parameter values and initial conditions.

3. Results

3.1.1. Differential equation model: absence of fire

In the absence of recurring fire or fire feedbacks, the two-state model has one stable equilibrium point at $(g, w) = (0, 1)$, which is a closed forest with no grass component. This solution is globally stable with the system returning to the equilibrium following any perturbation away from this point. No equilibrium points occur in a savanna state with both grass and trees, but two additional, unstable equilibria are present. The first is the solution located at $(g, w) = (0, 0)$, corresponding to the absence of both grass and woody vegetation. The second equilibrium is at $(g, w) = (1, 0)$, a grassland state, which is also unstable. The introduction of any tree biomass moves the system toward a closed forest state with the loss of the grass component. This means that within the context of our conceptual model, the two-state system is predicted to exist only as a closed forest in the absence of recurrent fire disturbance.

3.1.2. Differential equation model: grass feedback on fire

A feedback between grass abundance and fire frequency does not result in an equilibrium in a savanna state with coexisting grass and tree components. Two locally stable equilibria are possible: one equilibrium occurs in a grassland state without trees at $(g, w) =$
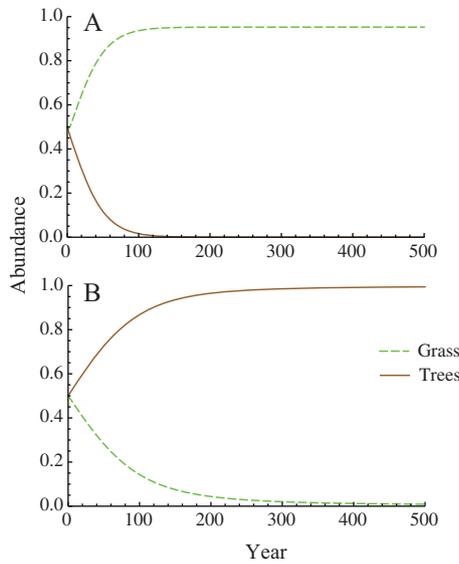
Fig. 2. A differential equation representation of a two-state savanna system with grass feedbacks on fire predicts that either grass (A) or trees (B) will dominate the system. Equilibrial savannas with grass and trees coexisting are not predicted by in this representation of the system (e.g., Eqs. (3) and (4)). The parameter values used in the simulations shown were $r_g = 1.5$, $r_w = 0.08$, $M_g = 0.05$, $M_w = 0.1$, $g_0 = 0.5$, and $w_0 = 0.5$ for both panels with c equal to 1.5 and 0.5 and for panels A and B, respectively.

$(r_g/(cM_g + r_g))$, 0 and is stable for some regions of parameter space (Fig. 2A). We do not provide an analytical expression guaranteeing stability but we do note that the condition $r_g < (cM_g r_w)/(cM_w - r_w)$ precludes a stable grassland. A second stable equilibrium occurs in a closed forest at $(g, w) = (0, 1)$ (Fig. 2B). This result indicates that a feedback between grass and fire can stabilize grasslands, but cannot maintain a mixture of trees and grasses in a savanna state.

3.2. Differential equation model with discrete fires

We illustrate two types of behavior in the differential equation model with discrete, stochastic fires. (i) The ecological community
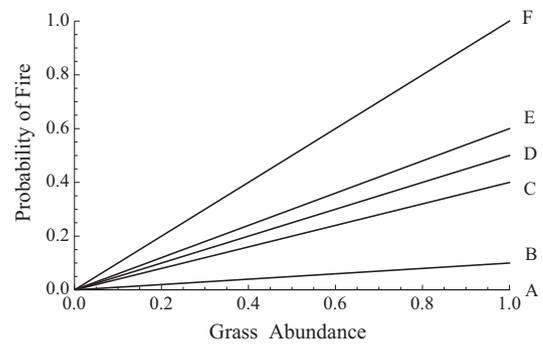

Fig. 4. The relationship between grass abundance and fire for simulations in Fig. 3. The lines of increasing slope represent the increasing strength of grass feedback on fire in panels A–F in Fig. 3. The strength of the grass feedback is given by c, where c is varied across 0, 0.1, 0.4, 0.5, 0.6, and 1.0 corresponding to panels A–F in Fig. 3. Fire is absent from the simulation in panel A in Fig. 3 and thus is represented by a horizontal line that is indistinguishable from the x axis here.

approaches either a forest (e.g., Fig. 3A–C) or grassland (Fig. 3D–F) state in some ranges of parameter space, as illustrated in Fig. 3. This behavior is similar to the results for the differential equation model described above. There are also regions of parameter space that display phase locking and long periods of transient behavior prior to approaching either a forest or grassland state (e.g., Fig. 3C and D), but a savanna state with coexisting grass and trees does not occur. The transitions in system behavior shown in Fig. 3 correspond to an increasing strength of the grass feedback on fire (Fig. 4). A grassland state is eventually attained as the grass feedback on fire strengthens. (ii) This model of the savanna system, however, can also exhibit a different behavior than observed in the differential equation model. While the system moves toward a forest state in the absence of fire (Fig. 5A) or with weak grass feedbacks on fire (e.g., Fig. 5B and C), a savanna state is eventually reached (Fig. 5E,F) as the grass feedback on fire increases (Fig. 6). In the corresponding region of parameter space, both the tree and grass components of the system are bounded within narrow ranges that reflect the pattern of biomass loss and regrowth associated with recurring fires (Fig. 5E and F).
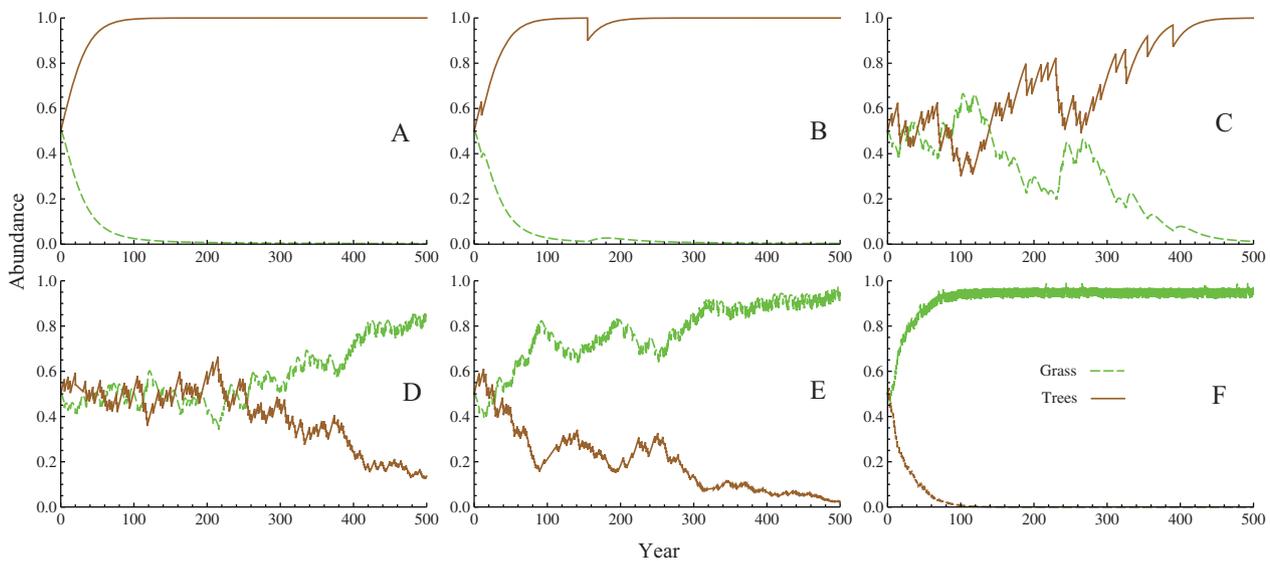

Fig. 3. Dynamics of grass and tree components based on a continuous differential equation model and probabilistic occurrence of discrete fires. The probability of fire is a linear function of grass biomass as illustrated in Fig. 4. Fire is absent from the system in panel A while panels B–F illustrate an increasing strength of feedback between grass biomass and fire probability. The system transitions from a forest state when fire is absent or infrequent to a grassland as the frequency of fire increases. Savannas with a mixture of grass and trees are not supported excepted during transients (e.g., panel D). The parameter values used for these simulations were $r_g = 1.5$, $r_w = 0.08$, $M_g = 0.05$, $M_w = 0.1$, $g_0 = 0.5$, and $w_0 = 0.5$ for all panels with c ranging from 0 to 1 as illustrated in Fig. 4.
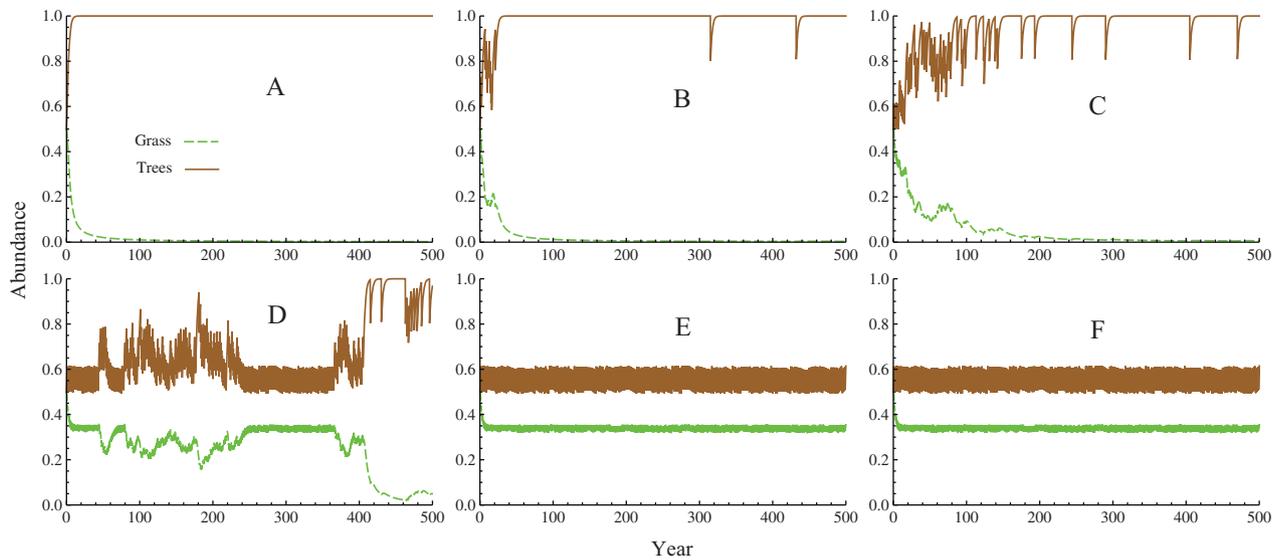
Fig. 5. Dynamics of grass and tree components based on a continuous differential equation model and probabilistic occurrence of discrete fires. The probability of fire is a linear function of grass biomass as illustrated in Fig. 6. Fire is absent from the system in panel A while panels B–F illustrate an increasing strength of feedback between grass biomass and fire probability. The system transitions from a forest state when fire is absent or infrequent to a savanna state when fire is frequent. Savannas with a mixture of grass and trees are supported by strong grass feedbacks on fire probability (e.g., panels E, F). The parameter values used for these simulations were $r_g = 0.5$, $r_w = 0.25$, $M_g = 0.1$, $M_w = 0.2$, $g_0 = 0.5$, and $w_0 = 0.5$ for all panels with c ranging from 0 to 10 as illustrated in Fig. 6.

3.3. Difference equation model

As the strength of the feedback between grass and fire probability increases in the differential equation model with fire as discrete events, fires become increasingly predictable and occur in nearly every year (e.g., Figs. 5 and 6). In this case, the differential equation model, (Eqs. (5) and (6)), with discrete fires approaches a difference model with a loss term applied in each time step (Eqs. (7) and (8)). This difference model has solutions in grassland $((g, w) = (1/(-1 + M_g)) + \lambda_g, 0)$, forest $((g, w) = 0, (1/(-1 + M_w)) + \lambda_w)$, and savanna states $((g, w) = ((1 + (-1 + M_g)\lambda_g + c(-1 + \lambda_w - M_w\lambda_w))/(-1 + M_g), (1/(-1 + M_w)) + \lambda_w))$. We verified the stability of these solutions as described in the methods. We additionally iterated this model to show that the difference model representation of the system can result in a stable savanna state as well as grassland or forest states (Fig. 7). These simulations confirm the results from Section 3.2, and suggest that the discreteness, rather than stochasticity, of fires allows for the savanna state.
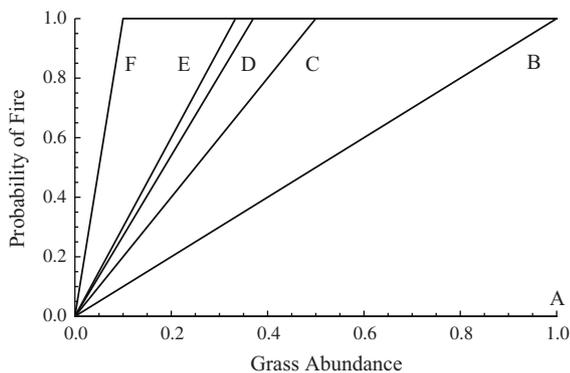

Fig. 6. The relationship between grass abundance and fire for simulations in Fig. 5. The lines of increasing slope represent the increasing strength of grass feedback on fire in panels A–F in Fig. 5. The strength of the grass feedback is given by c where c is 0, 1.0, 2.0, 2.7, 3.0, and 10.0 corresponding to panels A–F in Fig. 5. Fire is absent from the simulation in panel A in Fig. 5 and thus is indistinguishable from the x-axis here.

4. Discussion

We demonstrate the potential for grass feedbacks on fire to result in stable, equilibrial savanna communities containing both trees and grasses. Previous studies examining two- or three-state systems have indicated that grass-fire feedbacks do not result in savannas, but rather lead to grasslands or forests (e.g., D'Odorico et al., 2006; Beckage et al., 2009). We arrived at a different conclusion from an analysis of the same vegetation-fire feedbacks because of our use of a different modelling framework. We relaxed the assumptions inherent in a differential equation representation of these feedbacks by allowing fire to be a discrete event rather than a rate of biomass loss that is continuous in time. This latter assumption is embedded in the formulation of the model as a system of differential equations, but is not an accurate representation of the modeled system. The reduction in vegetation biomass in fire is a discrete event, followed by responses that require some minimum time to accumulate sufficient fuel to support a subsequent fire. As a result, biomass losses from fire are not continuous in time and fire may be more accurately represented in models as discrete events.

Discretization of fires in our savanna disturbance model results in grasses co-occurring with trees. The grass component of the ecological system persists in a temporal refuge resulting from the frequent removal of tree biomass by fire, and the resulting release of grasses from competition with trees (e.g., Scholes and Archer, 1997). This dynamic equilibrium results from two aspects of our model: (i) the asymmetric competition that favors trees at the expense of the grass layer results in the gradual displacement of grasses by trees in the absence of disturbance. (ii) Trees are either more strongly affected by fires (lose more biomass) and/or respond less quickly (regrowth of biomass) than the grass layer. The dynamic equilibrium with co-occurring grasses and trees thus results from recurrent fires that disproportionately affect trees, preventing the competitive exclusion of grasses by trees (e.g., House et al., 2003). In our model parameterization, a strong feedback of grass biomass on fire probability increases the likelihood that fires occur frequently enough to prevent trees from extirpating the grasses. Trees can thus be limited in the landscape without invocation of demographic bottlenecks that require differential effects
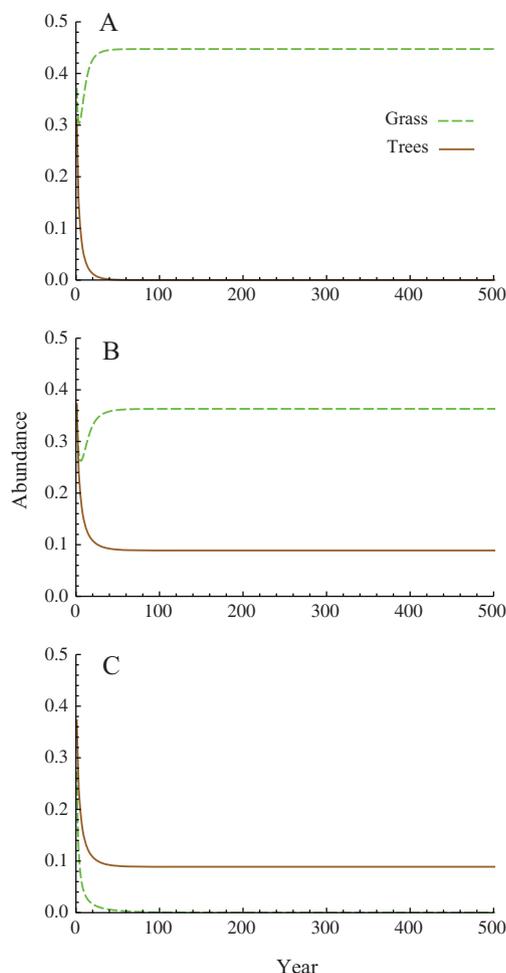
Fig. 7. A difference equation model representation of savannas can result in (A) grassland, (B) savanna, and (C) forest states. The difference model does not allow for stochasticity in fire occurrence but does model fire occurrence as a discrete events. The parameter values used for these simulations were $\lambda_g = 1.5$, $M_g = 0.05$, $g_0 = 0.5$, $\lambda_w = 1.0$, $M_w = 0.1$, $c = 1$, $w_0 = 0.5$ for panel A, $\lambda_g = 1.5$, $M_g = 0.05$, $g_0 = 0.5$, $\lambda_w = 1.2$, $M_w = 0.1$, $c = 1$, $w_0 = 0.5$ for panel B, and $\lambda_g = 1.1$, $M_g = 0.05$, $g_0 = 0.5$, $\lambda_w = 1.2$, $M_w = 0.1$, $c = 1$, $w_0 = 0.5$ for panel C.

of fire on and limitations in transitions between life history stages (Sankaran et al., 2004).

The dynamic relationship between savanna trees and grasses described above is an equilibrium in the sense that grass and trees co-occur while bounded between well-defined upper and lower limits (also see Jeltsch et al., 2000). We note that this dynamic equilibrium is different from a disequilibrium, where periodic but externally driven fire events can maintain a balance of grasses and trees in a savanna community (Sankaran et al., 2004; Beckage et al., 2006). Such a disequilibrium community could be considered a climatic equilibrium because the fire regime that maintains the disequilibrium is extrinsically determined by climatic conditions that determine the likelihood of fire events (e.g., Brenner, 1991; Beckage et al., 2003; Beckage et al., 2005; Bowman et al., 2009). Fire has been recognized as an important determinant of ecological communities (e.g., Bond et al., 2005), but fire regimes have been considered to be largely external to the savanna system (e.g., Brenner, 1991; Platt, 1999; Jeltsch et al., 2000; Beckage and Platt, 2003). Recurring fires can stabilize savanna systems in the absence of vegetation-fire feedbacks as long as long-term fire frequencies are maintained within specific bounds (Beckage et al., 2006). In contrast, the grass feedback on fire probability represents a control of fire frequency that is internal to the system: The grasses promote environmental

conditions (e.g., fire frequencies) that can bound the system in a savanna state. In this way, such fire-facilitating species can be considered ecosystem engineers that modify the characteristics of their environment (Jones et al., 1994, 1997) including fire regimes, with broad consequences for species diversity and community dynamics (Platt et al., 1988; Stout and Marion, 1993; Beckage and Stout, 2000; Gagnon et al., 2010).

Our analysis joins other analyses that have examined the influence of demographic assumptions on conclusions from savanna models (e.g., Hanan et al., 2008). We recognize, of course, that our results come from a mean field analysis that does not consider space, and that inclusion of space could result in a similar departure in consistency of model predictions. We are exploring the implications of spatial processes in a spatially explicit model of fire-vegetation dynamics in savanna systems (e.g., Beckage and Ellingwood, 2008). Our contrasting results for effects of a grass-fire feedback on savannas emphasize the importance of model formulation on understanding the dynamics of ecological systems (e.g., Durrett and Levin, 1994). We would alternatively conclude that a grass feedback on fire frequency does or does not support a savanna state, depending on how our model was constructed. Modeling fire as a discrete event, followed by a period of vegetation recovery, appears to be a critical assumption in our model formulation that results in the bifurcation of these results.

Acknowledgements

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