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Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states

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Abstract. Savannas are known as ecosystems with tree cover below climate-defined equilibrium values. However, a predictive framework for understanding constraints on tree cover is lacking. We present (a) a spatially extensive analysis of tree cover and fire distribution in sub-Saharan Africa, and (b) a model, based on empirical results, demonstrating that savanna and forest may be alternative stable states in parts of Africa, with implications for understanding savanna distributions.

Tree cover does not increase continuously with rainfall, but rather is constrained to low (<50%, "savanna") or high tree cover (>75%, "forest"). Intermediate tree cover rarely occurs. Fire, which prevents trees from establishing, differentiates high and low tree cover, especially in areas with rainfall between 1000 mm and 2000 mm. Fire is less important at low rainfall (<1000 mm), where rainfall limits tree cover, and at high rainfall (>2000 mm), where fire is rare. This pattern suggests that complex interactions between climate and disturbance produce emergent alternative states in tree cover.

The relationship between tree cover and fire was incorporated into a dynamic model including grass, savanna tree saplings, and savanna trees. Only recruitment from sapling to adult tree varied depending on the amount of grass in the system. Based on our empirical analysis and previous work, fires spread only at tree cover of 40% or less, producing a sigmoidal fire probability distribution as a function of grass cover and therefore a sigmoidal sapling to tree recruitment function. This model demonstrates that, given relatively conservative and empirically supported assumptions about the establishment of trees in savannas, alternative stable states for the same set of environmental conditions (i.e., model parameters) are possible via a fire feedback mechanism.

Integrating alternative stable state dynamics into models of biome distributions could improve our ability to predict changes in biome distributions and in carbon storage under climate and global change scenarios.

Key words: biome distribution; fire; forest; multiple stable states; rainfall; savanna; tree cover.

Introduction

The determinants of the distribution of the savanna biome are a matter of some debate. Traditionally, ecologists have treated savanna and forest distributions—and biome distributions, more broadly—as if they are rigidly determined by climate (Whittaker 1975, Breckle 1999, Woodward et al. 2004). However, modeling and experimental work have shown that mesic savannas can exist where climate, soils, and topography suggest forest should dominate (Swaine et al. 1992, Moreira 2000, Russell-Smith et al. 2003, Bond 2008). In Africa, climate constrains maximum tree cover, but tree cover varies substantially below that maximum (Sankaran et al. 2005), due to factors including fire and herbivory (Bucini and Hanan 2007, Bond 2008, Sankaran et al. 2008).

Biome models that include fire as a major determinant of tree cover perform better in predicting savanna and forest distributions than those based solely on climatic and edaphic inputs (Woodward et al. 2004, Bond et al. 2005, Scheiter and Higgins 2009). Fire exclusion experiments provide empirical evidence that fire can maintain a savanna where climatic and edaphic conditions could support a closed-canopy forest (Swaine et al. 1992, Moreira 2000, Russell-Smith et al. 2003). However, the effects of fire are strongly context dependent. Sankaran et al. (2005) showed that rainfall limits tree cover up to about 650 mm mean annual rainfall in Africa, but that fire can reduce tree cover below its potential (see also Bucini and Hanan 2007, Bond 2008, Sankaran et al. 2008).

For Africa, existing continental-scale analyses of the tree cover in savanna have focused only on savannas themselves (Sankaran et al. 2005, 2008, Bucini and Hanan 2007) and have been severely restricted in spatial and ecological extent (no data above 1200 mm rainfall [Sankaran et al. 2005]). A more comprehensive analysis

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of tree cover and of biome distributions in Africa is vital to a more complete understanding of the constraints on savanna distributions and the ecological dynamics that characterize savanna systems. Specifically, an analysis spanning the transition from savanna to forest is necessary for evaluating the processes that differentiate the two.

We analyzed spatial patterns of tree cover with respect to rainfall and fire frequency using satellite-derived data sets with complete spatial coverage of sub-Saharan Africa. These data allow analyses that were impossible in previous continental-scale analyses of tree cover; in particular, we can explore processes at the transition between forest and savanna.

Additionally, the data set allows an exploration of scale dependence of determinants of tree cover and biome distributions (Scanlon et al. 2007). Climatic determinants of biome distribution are often discussed at regional scales (Williams et al. 1996, Sankaran et al. 2005), while disturbances that reduce tree cover below its "climate potential" are usually considered as local processes (Sankaran et al. 2005). Explicit considerations of scale are included in our analysis of the savanna–forest boundary.

Because these results provide only correlative evidence for the importance of the drivers we identify, we have further evaluated the results of our continental-scale analysis of tree cover with an analytical and mechanistic model of tree–grass dynamics in savannas. This simple model invokes some basic assumptions about the ecology of fire in savannas to produce savanna and forest dynamics similar to those observed in our analysis. Together, the empirical observations and model presented in this paper should add to our theoretical and predictive understanding of the dynamics that constrain savanna and forest distributions.

Methods

We analyzed patterns of tree cover with respect to rainfall and fire frequency using satellite data. We derived fire frequency and tree cover from MODIS satellite reflectance data at 500-m resolution. We derived rainfall from the Tropical Rainfall Measuring Mission best-estimate precipitation product (TRMM 3B43), which has a resolution of 0.25° degrees (~28 × 28 km at the equator and 28 × 20 km at the southern tip of Africa).

1. *Tree cover*.—Percentage tree cover was calculated from the MOD44B Collection 3 product (Hansen et al. 2003). This product gives percent canopy cover (rather than the projected crown cover) at an appropriate scale and resolution for discriminating regional patterns (Miles et al. 2006, Bucini and Hanan 2007). A validation exercise in Zambia yielded root mean square errors (RMSE) of 5.2% (Hansen et al. 2002), although the RMSE of the global data set is estimated at 9.1%. This error decreases substantially when data are averaged over slightly larger scales because geolocation issues account for most error (Hansen et al. 2003). The product was only calibrated against trees >5 m tall and may underestimate shrubby species.

2. *Fire frequency*.—We used the monthly MCD45A1 burnt area product to derive an estimate of fire frequency (Roy et al. 2008). MCD445A1 uses change detection procedures based on a bi-directional reflectance distribution function (BRDF) to identify burn scars in the landscape, and identifies burnt areas in Africa with high accuracy (R^2 = 0.75 [Roy et al. 2008]). Improved resolution (500 m instead of 1 km) and information on data quality make this product more reliable than previous burnt area products. An independent validation by Tsela et al. (2010) across biomes demonstrated that accuracy is higher in open systems ($R^2 = 0.86$) and lower in pine plantations ($R^2 = 0.38$); fires <500 × 500 m in size could be detected, but at lower probability. For this analysis, monthly data layers from April 2000 to March 2008 were combined to calculate the number of times a pixel burned in eight years (fire frequency). Pixels with invalid data more than two times a year on average were excluded based on quality flags. This yielded a 500-m resolution map of number of burns in eight years (ranging from 0 to 13). Savanna fires are grass fuelled, with average return times ranging from two to six years (van Wilgen and Scholes 1997); while an eight-year data set is short, the data set does span the range of fire frequencies expected in the system.

3. *Rainfall*.—The TRMM combines satellite data, rain gauge data, and precipitation models to produce a best estimate of global precipitation at hourly to annual scales. A validation by Nicholson et al. (2003) over West Africa demonstrated a root mean square error of 0.7 mm/d and a zero bias, although subsequent validations indicated that it is less accurate in topographically variable landscapes (Dinku et al. 2007). In this analysis, spatially explicit monthly precipitation rates were summed to produce annual rainfall for each year (1998–2007) and then averaged to estimate mean annual rainfall (MAR).

These data sets, reprojected to an Albers equal area projection, were clipped at 15 degrees north to include only sub-Saharan Africa. Fire and tree data were resampled to align with the larger-scale TRMM data. They were then progressively degraded to produce maps of average tree cover and average fire frequency at 500-m, 1-km, 2.5-km, 5-km, 10-km, 25-km, 50-km, and 100-km resolution. Rainfall data were not available for fine scales (resolution less than ~25 km). However, we have included smaller scales because tree cover does vary at these scales, while rainfall varies over regional to continental scales. To reduce potential pseudo-replication, we have subsampled plots at scales <25 km to include only the center plot of each 25-km block (i.e., only one tree cover measurement per rainfall measurement).

Rainfall and fire data have been included for the longest available time period, despite the fact that this has resulted in mismatched time periods for the data. This inclusion has allowed us to establish the most

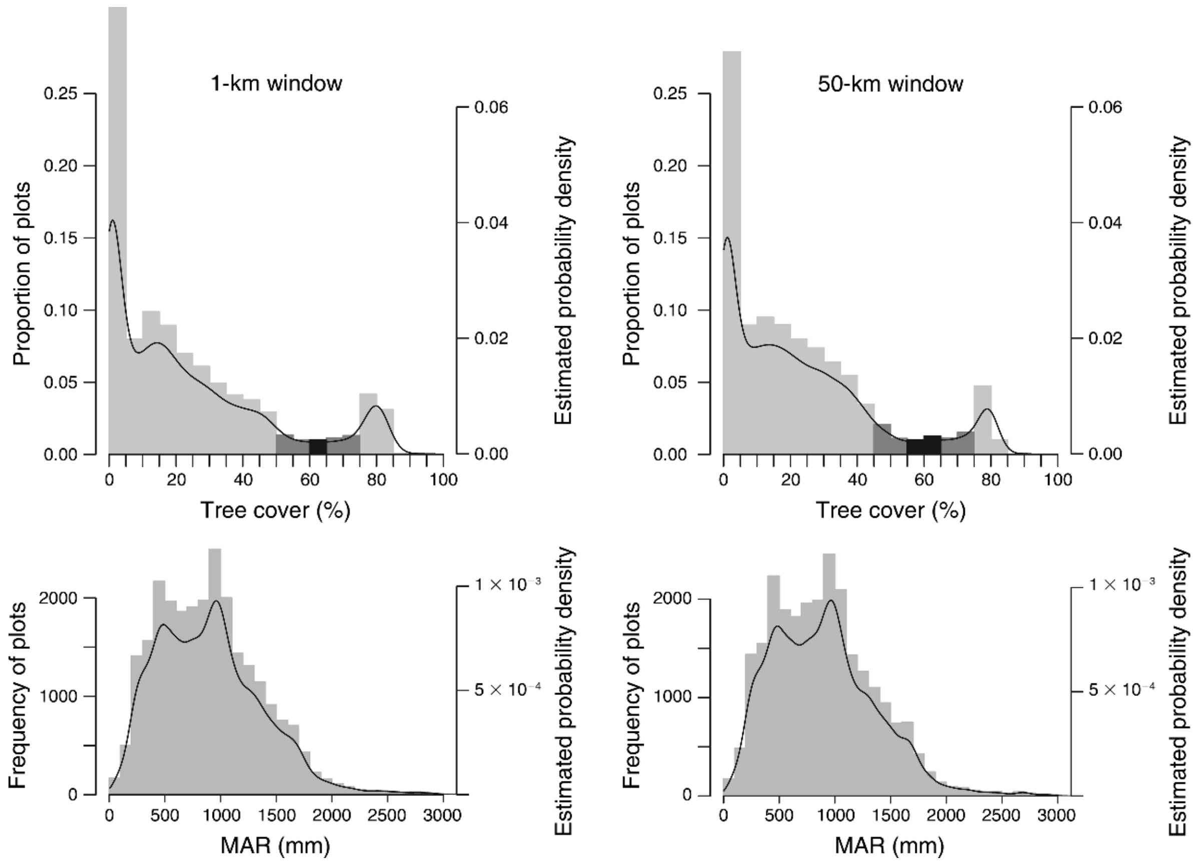

FIG. 1. Histograms of tree cover (%; top) and mean annual rainfall (MAR; bottom) at 1-km (left) and 50-km scales (right). For histograms of tree cover, dark gray bars denote categories with proportion of plots with values <2.5%; black bars denote the midpoint of the range of dark gray bars. The curves represent the estimated probability density of plots.

rigorous possible estimates for long-term mean annual rainfall and fire frequency across sub-Saharan Africa.

The centroid of each TRMM pixel was used to create a regular grid of 22 726 sampling points over sub-Saharan Africa. Rainfall, average percent tree cover, and average fire frequency were extracted at each point for each scale of analysis. At resolutions of 50 km and 100 km, which are larger than a TRMM pixel, the number of unique data points available was reduced to 6982 and 1751, respectively, but at smaller scales, all of the available sampling points were used.

All analyses were run at all scales. We chose 1-km and 50-km scales for presentation, but this choice has no qualitative impact on the findings presented herein. Data were extracted in ERDAS 9.3 and ArcGIS 2.8.1 and analyzed in R 2.8.1 (R Development Core Team 2008). Generalized additive model (GAM) fitting was done with a Gaussian link function using the R package mgcv 1.4-1.1 (Wood 2008).

RESULTS AND DISCUSSION

Are savanna and forest distinct states?

Frequency distributions of tree cover across sub-Saharan Africa showed two clear maxima at ~15% and 80% cover with a frequency minimum at ~60%; rainfall did not show a similarly bimodal distribution (Fig. 1). The lower of these tree cover peaks represents savanna, the higher peak forest. Sites with intermediate tree cover (50–75%) were rare (density <5%), although the corresponding range of rainfall occurs frequently. Pixel-scale data were split into savanna and forest subsets based on the midpoint of the minimum interval. This midpoint was consistent across scales, ranging between 60% and 62.5% tree cover, with the savanna peak ending around 40–50% tree cover.

The distribution of savanna and forest tree cover classes along a rainfall gradient indicates that savannas can occur at MAR of up to 2000 mm per year and that forests occur frequently at MAR as low as 800–1000 mm per year (Fig. 2). Precipitation thresholds for each type were defined where the proportion of plots in the class fell below 1% (descending the precipitation gradient for forests, ascending for savanna). Thresholds were constant across scales from 500 m to 100 km. To further evaluate the range of rainfall at which two alternative states were present, we divided sites into 200-mm rainfall classes. Tree cover is distinctly bimodal

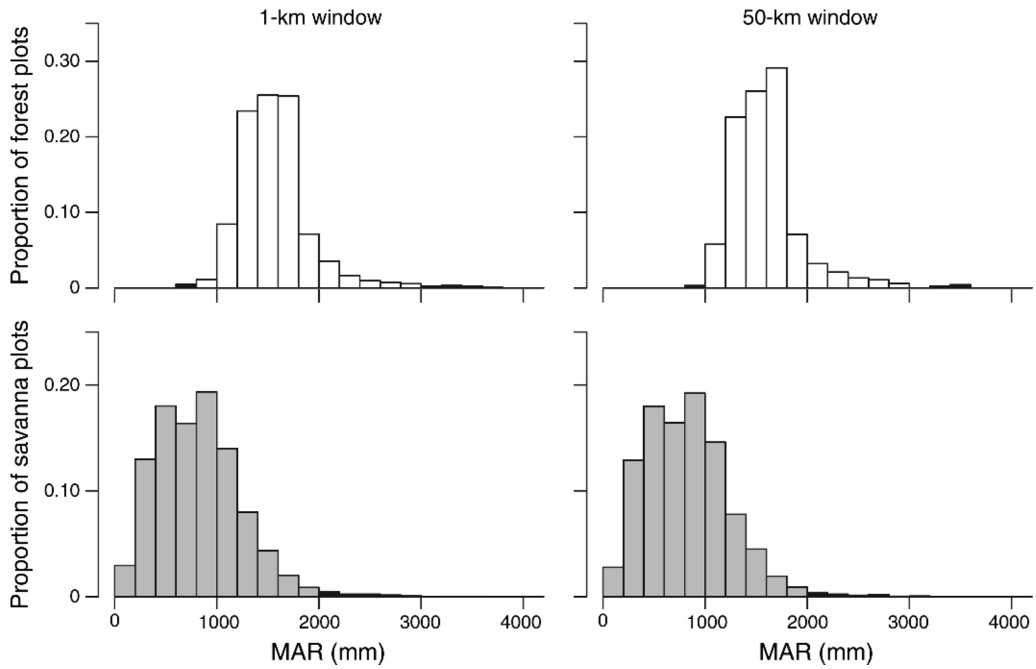

FIG. 2. Histograms of savanna (top) and forest (bottom) vs. mean annual rainfall (MAR) at 1-km (left) and 50-km scales (right). Savanna had <62.5% or <60% and forest had >62.5% or >60% tree cover at 1-km and 50-km scales, respectively. Black bars denote frequency with values <1%.

between MAR 1000 mm and 2000 mm at all scales (see Fig. 3 for 1-km scale).

Plotting predictions of tree cover vs. rainfall (Fig. 4 and Table 1) shows that tree cover was strongly related to rainfall only at low rainfall (<1000 mm) and at high rainfall (>2000 mm). At all intermediate rainfall levels, climate can apparently support forest, but savanna persisted over large areas.

These thresholds for the minimum rainfall that supports forest (1000 mm MAR) and the maximum rainfall at which savannas occur (2000 mm MAR) differ somewhat from previous estimates calculated from field data, which put the lower limit of forest at 650 ± 125 mm MAR and did not define a maximum rainfall for savannas (Sankaran et al. 2005). However, the 1000-mm minimum rainfall threshold for canopy closure (forest) is consistent with a continental analysis of fire exclusion experiments by Bond et al. (2005). Below 1000 mm annual rainfall, fire exclusion resulted in increases in woody cover but not in a transition to closed-tree canopy forest, while above 1000 mm annual rainfall, fire exclusion resulted in a transition from savanna to forest (Bond et al. 2005). This analysis focuses on tree cover rather than on woody cover; processes that lead to high woody cover at lower rainfall generally do not result in high tree cover and, while important to land managers, can not be explored by this framework. Interestingly, in South American examples, savanna persisted up to 1400 mm rainfall in fire exclusion experiments, suggesting that a continental comparison of the processes that differentiate savanna from forest might be fruitful.

Evidence of stabilizing feedbacks

At intermediate rainfall (1000–2000 mm MAR), tree cover was strongly reduced when fire was present. Below 1000 mm MAR savanna could persist without fire. Fire did not occur frequently above 2000 mm MAR (Fig. 4). Including the presence/absence of fire as a categorical variable in generalized additive models of mean annual rainfall on tree cover improved model fit significantly across all scales (Table 1). Again, results were scale invariant; GAMs including both rainfall and fire explained between 54% (at fine scales) and 76% (at coarse scales) of the variation in tree cover. These analyses indicate that, depending on rainfall, fire was probably an important stabilizing feedback operating in savannas.

Fire does not fully explain variation in tree cover response to rainfall. In part, this may be because the available satellite fire record only spans the last eight years. However, other drivers (e.g., herbivory, nutrient cycling, hydrology, human activity) that are difficult to quantify remotely may also contribute. In addition, this analysis cannot determine whether fire promotes savanna or vice versa. Both are likely. We know from fire exclusion experiments around the world that fire reduces tree cover (Swaine et al. 1992, Moreira 2000, Russell-Smith et al. 2003). We also know that grass biomass drops off rapidly as tree cover increases (Scholes 2003, Lloyd et al. 2008), such that fires can only spread in systems with tree cover of less than ~40% (Hennenberg et al. 2006, Archibald et al. 2009). These relationships

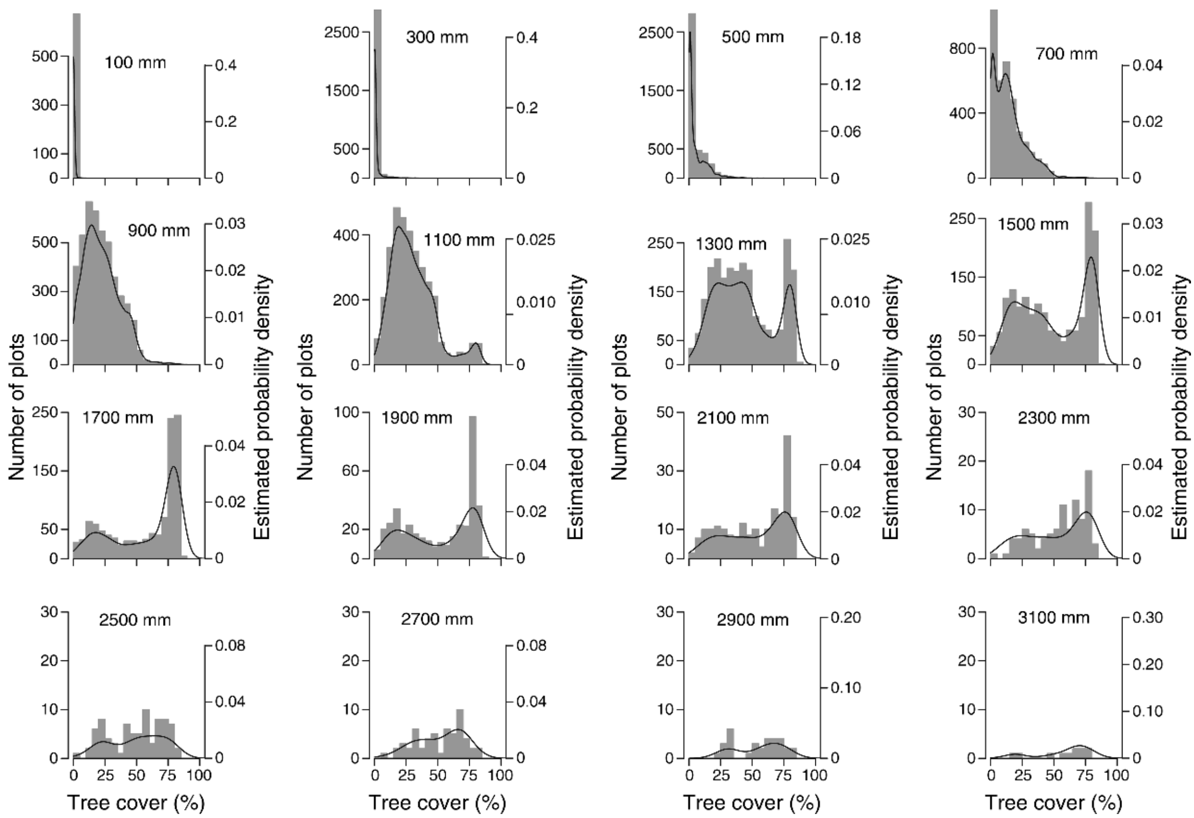

FIG. 3. Histograms of percent tree cover categorized by rainfall at the 1-km scale. Each plot includes data from a 200-mm range in rainfall and is named with the midpoint of that range. Curves represent estimated probability density of plots.

suggest a stabilizing feedback contributing to maintenance of savanna and forest as alternative stable states at intermediate rainfall.

MODEL DESCRIPTION AND RESULTS

Our analysis of the distribution of tree cover in sub-Saharan Africa provides correlative evidence (a) that rainfall constrains tree cover below 1000 mm mean annual rainfall (MAR), (b) that savanna and forest are distinct states that are both frequent at intermediate rainfall, and (c) that forest dominates strongly above 2000 mm MAR. Evaluating the stability of these distinct states is not possible from these short-term data. However, we have incorporated the fire feedback mechanism suggested by our empirical analysis into a simple model to evaluate the potential for savanna and forest to exist as alternative stable states.

The model is nonspatial but we have, in effect, created limited space by holding the total area of grass (G), tree saplings (S) and adult trees (T) constant (see Fig. 5). Grass is the default type and occupies all areas not explicitly occupied by saplings or trees. Saplings establish in proportion to the number of trees in the system, and can only establish in units occupied by grass (rate constant β). Trees recruit from saplings at a rate $\omega(G)$ in proportion to the number of saplings. The recruitment rate $\omega(G)$ varies with grass as described below. Both saplings and trees die and revert to grass in proportion to their number (rate μ and ν). The model is formally described by the following set of coupled differential equations, which always add to zero (since $G + S + T =$ total area):

$$\frac{dG}{dt} = \mu S + \nu T - \beta G T \tag{1}$$

$$\frac{dS}{dt} = \beta G T - \omega(G)\, S - \mu S \tag{2}$$

$$\frac{dT}{dt} = \omega(G)\, S - \nu T. \tag{3}$$

Our model incorporates two fundamental assumptions about savanna ecology. First, based in part on our findings from this study, we assume that fire spread in savannas depends on grass abundance, as reflected in the function $\omega(G)$. Savannas with tree cover below ~40% burn frequently, but fire is almost nonexistent in systems with tree cover above the 40% threshold (Archibald et al. 2009). We can incorporate this nonlinear response of fire frequency to grass abundance via $\omega(G)$, the recruitment of saplings into trees. Fire rarely kills savanna tree saplings, which are able to resprout after

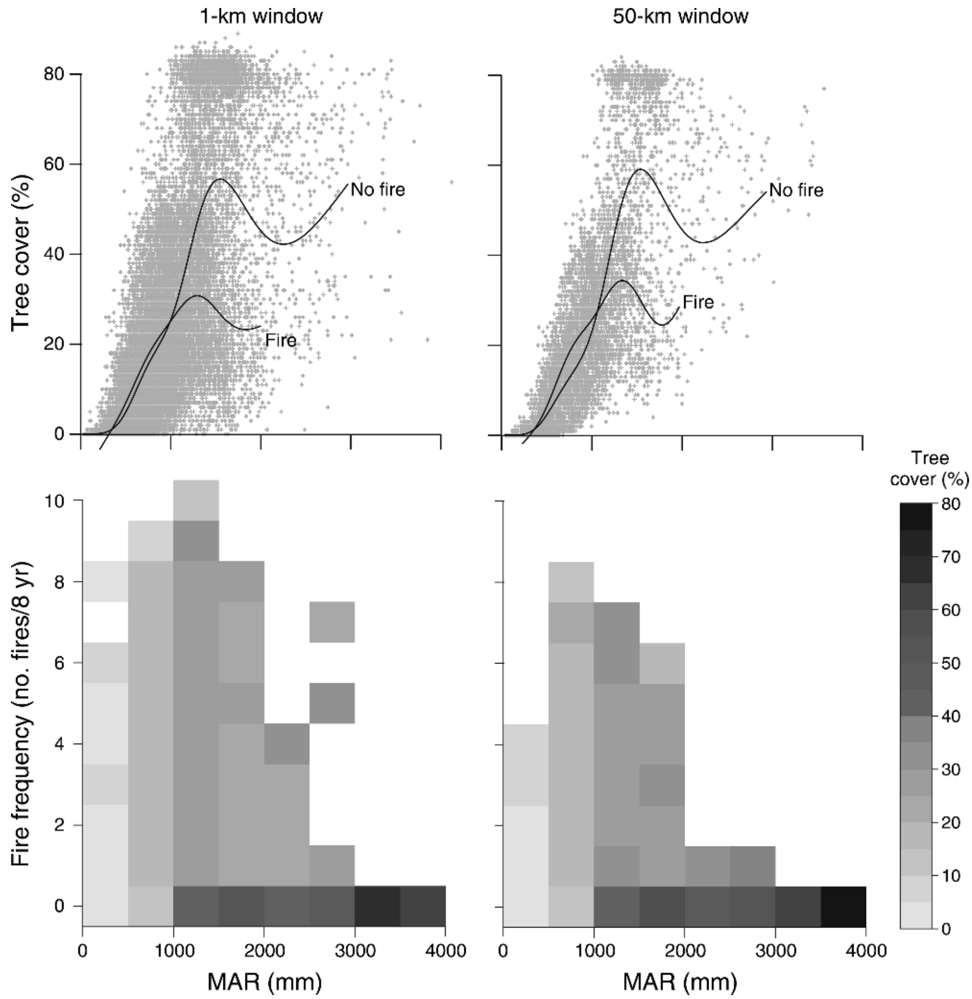

FIG. 4. Effects of rainfall and fire on tree cover in sub-Saharan Africa. (Top panels) tree cover vs. mean annual rainfall at 1-km and 50-km scales. Curves represent fits from generalized additive models including rainfall and fire presence as variables (Table 1); fits are significant at both the 1-km ($R^2 = 0.574$, $P < 0.001$) and the 50-km scale ($R^2 = 0.673$, $P < 0.001$). (Bottom panels) mean percent tree cover vs. rainfall and fire frequency at 1-km and 50-km scales.

fire (Bond and Midgley 2001, Hoffmann et al. 2009, Schutz et al. 2009), and it infrequently affects adult trees (Hoffmann and Solbrig 2003). Fire does impose a major control on the recruitment of tree saplings into adults (Higgins et al. 2000, Hoffmann et al. 2009). Taken together and averaged over time, these features of savanna systems mean that tree recruitment should be high when grass abundance (and fire frequency) is low, should fall off rapidly near 40% tree cover, and should remain low at high grass abundance (see Fig. 5). We make no assumptions about $\omega(G)$ other than smoothness and its general sigmoidal shape.

To solve for equilibria, we set each of Eqs. 1, 2, and 3 equal to zero. One solution is the trivial $S = T = 0$, but there are also internal equilibria defined by the following condition:

$$\omega(\bar{G}) = \frac{\mu\nu}{\beta\bar{G} - \nu}. \quad (4)$$

For convenience, define

$$f(G) = \frac{\mu\nu}{\beta\bar{G} - \nu}. \quad (5)$$

Internal equilibrium points are thus points where

$$\omega(\bar{G}) = f(\bar{G}). \quad (6)$$

The stability of the equilibria depends on the relative slopes of these two functions, as shown below.

Since $S + G + T = 0$, we can eliminate Eq. 2 and analyze the stability of equilibria by constructing the following Jacobian matrix:

$$J = \begin{bmatrix} -\Big(\nu + \omega(G)\Big) & S\omega'(G) - \omega(G) \\ \nu - \beta G - \mu & -(\mu + \beta T) \end{bmatrix}. \quad (7)$$

It can be shown via application of the Routh-Hurwitz stability criteria that the eigenvalues of the Jacobian have negative real parts (i.e., the equilibrium is stable,

Table 1. Results of generalized additive models fitting tree cover to rainfall and fire presence.

Scale (km)	Model†	R^2	N	GCV	Factor	Statistics F or t	Statistics df	Statistics P	Fire improved fit? F	Fire improved fit? df	Fire improved fit? P
0.5	tree cover ~ MAR	0.500	22 521	232.4	MAR	2434	8.74	<0.001			
	tree cover ~ MAR × fire	0.541		213.6	fire pres./abs.	1.566		0.117	225.5	22 502, 8.88	<0.001
					MAR × fire	221.3	8.24	<0.001			
					MAR × no fire	2473	9.38	<0.001			
1	tree cover ~ MAR	0.532	22 794	211.2	MAR	2790	8.78	<0.001			
	tree cover ~ MAR × fire	0.574		192.3	fire pres./abs.	1.414		0.679	292.2	22 776, 7.73	<0.001
					MAR × fire	284	7.09	<0.001			
					MAR × no fire	2866	9.42	<0.001			
2.5	tree cover ~ MAR	0.551	22 746	191.3	MAR	2999	8.80	<0.001			
	tree cover ~ MAR × fire	0.600		170.5	fire pres./abs.	1.166		0.244	322.7	22 728, 8.65	<0.001
					MAR × fire	324.5	8.00	<0.001			
					MAR × no fire	3121	9.45	<0.001			
5	tree cover ~ MAR	0.565	22 778	179.2	MAR	3170	8.82	<0.001			
	tree cover ~ MAR × fire	0.613		159.4	fire pres./abs.	0.229		0.819	342.7	22 760, 8.29	<0.001
					MAR × fire	399.6	7.64	<0.001			
					MAR × no fire	3242	9.47	<0.001			
10	tree cover ~ MAR	0.577	22 759	168.9	MAR	3328	8.82	<0.001			
	tree cover ~ MAR × fire	0.625		149.6	fire pres./abs.	0.939		0.348	353.5	22 741, 8.36	<0.001
					MAR × fire	439.6	7.73	<0.001			
					MAR × no fire	3378	9.45	<0.001			
25	tree cover ~ MAR	0.597	22 757	155.4	MAR	3612	8.84	<0.001			
	tree cover ~ MAR × fire	0.652		134.1	fire pres./abs.	0.770		0.441	420.1	22 739, 8.62	<0.001
					MAR × fire	526	7.99	<0.001			
					MAR × no fire	3718	9.47	<0.001			
50	tree cover ~ MAR	0.615	22 703	144.9	MAR	3878	8.85	<0.001			
	tree cover ~ MAR × fire	0.673		123.0	fire pres./abs.	3.98		<0.001	416.6	22 683, 9.79	<0.001
					MAR × fire	550.1	9.16	<0.001			
					MAR × no fire	4014	9.47	<0.001			
100	tree cover ~ MAR	0.638	22 570	131.2	MAR	4249	8.87	<0.001			
	tree cover ~ MAR × fire	0.711		105.0	fire pres./abs.	5.96		<0.001	562.8	22 550, 10.0	<0.001
					MAR × fire	655.9	9.36	<0.001			
					MAR × no fire	4647	9.55	<0.001			
250	tree cover ~ MAR	0.670	22 398	108.0	MAR	4813	8.96	<0.001			
	tree cover ~ MAR × fire	0.763		77.6	fire pres./abs.	7.03		<0.001	877.1	22 378, 10.0	<0.001
					MAR × fire	1173	9.39	<0.001			
					MAR × no fire	5731	9.59	<0.001			

Notes: Results are presented for models fitted without and with fire and for ANOVA/GCV (Generalized Cross Validation) testing whether adding fire improved model fit.

† The notation "tree cover ~ MAR" means that tree cover is the dependent variable with MAR as the independent variable.

ignoring the marginal case of zero real parts) if and only if the trace of the matrix is negative and the determinant positive (Edelstein-Keshet 2005).

For this system, the eigenvalues of the Jacobian are always real, and the condition on the trace is trivially satisfied. The condition on the determinant is satisfied when

$$\omega'(\bar{G}) > \frac{-\beta\mu\nu}{(\beta\bar{G}-\nu)^2} = f'(\bar{G}). \tag{8}$$

This stability condition makes a graphical analysis of this system of equations intuitive (Fig. 5). Where plots of $\omega(G)$ and $f(G)$ intersect, equilibria exist. Those equilibria are stable when the slope of $\omega(G)$ is greater than the slope of $f(G)$. Note that we have made no assumptions about the functional form of $\omega(G)$ in our analysis. However, its functional form will determine the number and stability of equilibria that define the system, and for illustrative purposes we henceforth assume that $\omega(G)$ is sigmoidal. Depending on the values of rate constants, the dynamic system of equations then has between zero and three internal equilibria, with between zero and two stable internal equilibria (Fig. 5). Crucially, this sigmoidal form for $\omega(G)$ makes multiple stable equilibria possible. This simple model, based on empirically well-supported assumptions about fire and tree establishment in savannas, suggests that the savanna and forest patterns observed in our empirical analysis of tree cover actually are alternative stable states. In addition, this model suggests that a positive fire feedback within savanna is a sufficient mechanism for promoting alternative stable states. The model also captures situations in which only one stable equilibrium exists, at either low or high grass cover.

Conclusions

These empirical and modeling results indicate that savanna and forest may reasonably be interpreted as alternative states at intermediate rainfall. At low rainfall, fire does not play a major role in determining tree cover. At intermediate rainfall (between 1000 and 2000 mm), interactions between rainfall and fire produce

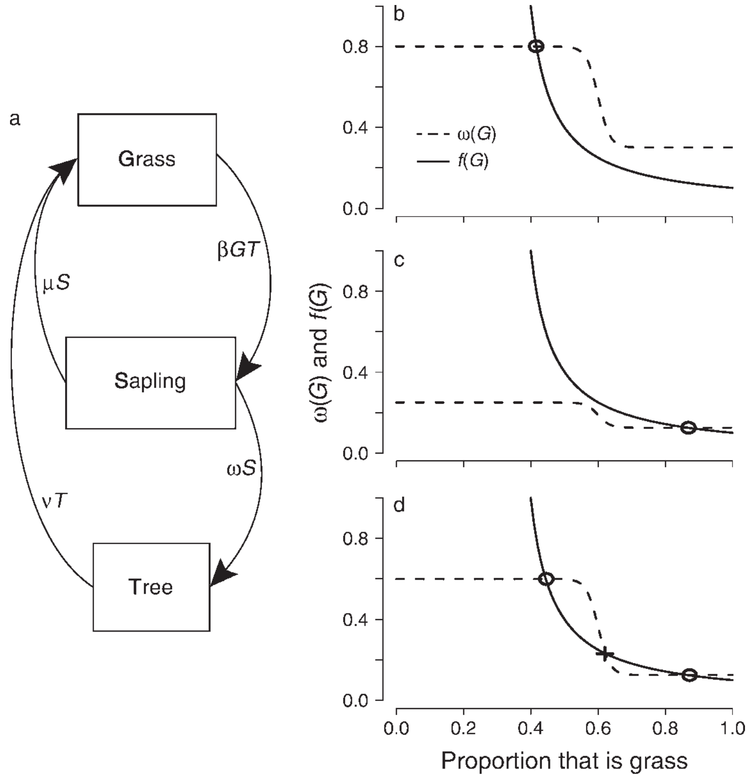

FIG. 5. (a) Model outline and (b–d) graphical analyses of the model, where β is the birth rate of savanna saplings, ω is the rate of transition of savanna saplings to savanna trees, μ is the death rate of savanna saplings, and ν is the death rate of savanna trees. The expression $f(G)$ is a function of these fundamental rates and is defined by Eq. 3. Equilibria exist where $\omega(G) = f(G)$ (Eq. 4). Equilibria are stable where $\omega'(G) > f'(G)$ (Eq. 8) (stable equilibria are denoted by open ovals; an unstable equilibrium is indicated by a "+" symbol). There are between 0 and 3 internal equilibria and between 0 and 2 stable internal equilibria, e.g., (b) a stable low-grass equilibrium, (c) a stable high-grass equilibrium, and (d) stable high- and low-grass equilibria.

discontinuities in tree cover, with alternative savanna and forest states. At high rainfall, fire is rare and forests dominate. Moreover, savannas appear to have tree cover up to only ~40–50%, consistent with studies that have found that grass productivity becomes negligible at tree cover >50% (Lloyd et al. 2008).

Ecosystems subject to multiple stable states have distinct configurations under the same set of environmental conditions, as in the model presented here. Multiple stable states are not possible without stabilizing feedbacks that function within a state to maintain it (Sternberg 2001, Scheffer and Carpenter 2003). Transitions among stable states occur when feedbacks break down or when environmental changes exceed thresholds (Carpenter et al. 1985, Scheffer et al. 1993, van de Koppel et al. 1997). Those transitions are often rapid and are not reversible on short time scales (Scheffer and Carpenter 2003).

Savanna and forest have sometimes been modeled as alternative stable states (Sternberg 2001, Favier et al. 2004*a*, Beckage et al. 2009, Accatino et al. 2010, Higgins et al. 2010), but empirical evidence has so far been lacking at the continental scale. Paleoecological studies have shown that rapid changes between tree-dominated and grass-dominated systems are common (Gillson 2004), but these span time scales at which climate has varied substantially. The discontinuity in the transition from savanna to forest (Hennenberg et al. 2006, Pueyo et al. 2010) also suggests alternative stable state dynamics, but existing continental analyses of tree cover have shown only that tree cover in savannas is variable (Sankaran et al. 2005, 2008, Bucini and Hanan 2007).

Within savanna, a number of factors, including fire, might result in stabilizing feedbacks. Fire suppresses tree cover (Swaine et al. 1992, Moreira 2000), probably by limiting recruitment of saplings to trees (Hoffmann 1999, Higgins et al. 2000). Similarly, there seems to be a threshold above which tree cover (i.e., insufficient grass) suppresses fire (Hennenberg et al. 2006, Archibald et al. 2009). While other factors influence tree emergence, and the data presented here yield an essentially correlative result, our combination of empirical analysis and modeling supports the sufficiency of rainfall–fire interactions for maintaining savanna and forest as alternative stable states at the continental scale. However, scale-invariance of these results suggests that processes that produce these patterns operate locally (Scanlon et al. 2007).

Interpreting savanna and forest as alternative stable states makes understanding the transitions between savanna and forest important. We know, from fire exclusion experiments (Swaine et al. 1992, Moreira 2000, Russell-Smith et al. 2003) and documentation of forest encroachment from around the world (Loehle et al. 1996, Bowman et al. 2001, Favier et al. 2004*b*, Goetze et al. 2006, Mitchard et al. 2009), that changing burning practices and patterns through landscape fragmentation and management policy have resulted in widespread encroachment of forest into savanna.

However, transitions from forest to savanna in the absence of anthropogenic deforestation are less well understood. Paleoecological work suggests that contemporary savannas established in areas that are now wet enough to support forest during a period with drier climatic conditions (Desjardins et al. 1996). This hypothesis fits well with the alternative stable state framework presented here, wherein forest could be converted to savanna when rainfall decreased to below 1000 mm. Savanna might then be stable even if rainfall increased. In fact, C4 grass evolution and the global expansion of savanna occurred during the Miocene, a period marked not only by aridity but also by increased rainfall seasonality (Keeley and Rundel 2005). A similar rainfall–fire interaction mechanism has been invoked to explain some of the dynamics at the prairie–forest ecotone in the northern United States (Grimm 1983, 1984).

Global projections indicate that rainfall and fire frequency will change in coming decades due to increasing atmospheric CO_2 and associated climate change. These changes may result in major biome shifts in favor of savanna over forest. Recent work has suggested that the Amazon rain forest may be at risk of severe drying (Phillips et al. 2009), putting large areas that are currently forest at risk of a transition to savanna. Our results imply that changes in biome distribution in response to climate change will not result in smooth transitions from savanna to forest or back. We can expect changes to be sudden.

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