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Dynamic response of grass cover to rainfall variability: implications for the function and persistence of savanna ecosystems

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Abstract

Savanna grass cover is dynamic and its annual extent resonates with wet season rainfall, as shown by satellite observations of normalized difference vegetation index (NDVI) time series for the Kalahari Transect (KT) in southern Africa. We explore the hydrological significance of the dynamic grass cover by applying a soil moisture model to the water-limited portion of the KT, which spans a north-south gradient in mean wet season rainfall, $\bar{r}$, from approximately 700 to 300 mm. Satellite-derived tree fractional cover, x_t, is shown to be highly correlated with ground meteorological measurements of $\bar{r}(R^2 = 0.94)$ in this region. By implementing a simple expression for grass growth and decay in the model that factored in only x_t and near-surface soil moisture, we were able to effectively reproduce the satellite-derived fractional grass cover, x_g, along the transect over a 16-year period (1983–1998). We compared the results from dynamic grass model with those yielded by a static grass cover model in which x_g was set to its 16-year average for each simulation. The dynamic quality of the grass was found to be important for reducing tree stress during dry years and for reducing the amount of water that is lost from the overall root zone during the wet years, relative to the static grass case. We find that the dynamic grass cover acts as a buffer against variability in wet season precipitation, and in doing so helps to maximize ecosystem water use. The model results indicate that mixed tree/grass savanna ecosystems are ideally suited to reach a dynamic equilibrium with respect to the use of a fluctuating limiting resource (water) by having functional components that respond to variability in rainfall over long timescales (trees) and short timescales (grasses).
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1. Introduction

Savanna ecosystems, characterized by their mixed tree/grass [1] composition, are common throughout many semi-arid regions of the world and can persist for thousands of years, as inferred from pollen records [43]. Ecologists are prone to cite fire [7,22,24], herbivory [5,14], or their combined effect [4,28,54] as the primary factors that prevent these mixed compositional ecosystems from being transformed into their forest or grassland end members. Hydrological aspects, however, should not be necessarily dismissed in terms of promoting the persistence of these systems that are often water-limited. Evidence of water limitation on savanna vegetation growth is found at the plot scale [25,52] up

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  [1] The term "trees" is used throughout the text as a general designation for woody vegetation, including trees and shrubs, while the term "grass" here refers to herbaceous vegetation, including grasses and forbs.

to the regional scale, where time series of satellite data have shown that interannual fluctuations in normalized difference vegetation index (NDVI), a measure of vegetation "greenness", resonate with wet season rainfall amounts most prominently in areas of savanna vegetation cover [23]. Much of this interannual variability in NDVI can be attributed to the grass component of the tree/grass mixture due to the grass cover growth characteristics [46]. The dynamic nature of grass growth is clearly a significant feature of savanna ecosystems, yet its influence on savanna function has been largely overlooked in previous analyses. Here, we apply a modeling framework to evaluate the ecohydrological role of observed grass dynamics and explore the implications the overall vegetation water use in terms of the persistence of savanna ecosystems.

As noted in a recent review [3], the dynamical growth aspect of vegetation is frequently disregarded in the implementation of land surface hydrological models. For certain vegetation types and timescales of interest, this may indeed be an appropriate simplifying assumption. In many other cases, however, the inclusion of vegetation dynamics in the model framework may be deemed essential. The decision on how best to treat modeled vegetation can have implications beyond simply the degree and level of detail to which one wishes to reproduce the physical processes; indeed, the theoretical underpinnings of the model interpretation are affected as well. For example, in the modeling of tree/grass coexistence in savanna ecosystems as a function of hydrological controls, a static view of the vegetation will lead to equilibrium solutions for the vegetation composition [17,56], whereas a conceptualization that includes variable growth must necessarily seek a "dynamic equilibrium" in which the transient state of vegetation is governed by variable climatic forcings. In the latter case, optimal vegetation assemblages with respect to water use arise as a consequence of not only the mean, but also the variability in wet season rainfall.

The fact that land surface hydrological model complexity has often been constrained by disregarding grass dynamics can be attributed, in part, to the absence of observations that would otherwise prompt its inclusion. Field investigations are usually limited to short-term, plot scale studies that lack both the temporal and spatial coverage needed to characterize grass dynamics directly in a comprehensive manner. Recently, this data deficit has been addressed through remote sensing methods to quantify grass cover in space and time [16,46,47]. Observations from satellite data, in fact, motivated the present analysis and are used to characterize vegetation cover for the regional-scale land surface hydrological model presented herein.

Any modeling effort in examining the relationship between moisture availability and savanna vegetation structure must rely upon an a priori conceptualization of water use for trees and grasses. Commonly invoked is the Walter hypothesis [57], in which the vertical juxtaposition of rooting depths provides a niche separation for water uptake, thus leading to the emergent mixed tree/grass savanna structure. Grasses are considered to be intensive exploiters, able to out-compete trees for soil moisture in the upper soil layer, while trees are characterized as being extensive exploiters, having preferential access to water at greater depth. Although the Walter hypothesis has been criticized by some for providing an oversimplified depiction of the root zone profiles [32,51], as pointed out by [8] there have been a number of other field studies that have reported its appropriateness and its use in modeling studies has remained prevalent. Indeed, there is a general agreement that vertical niche separation is a relevant feature of savanna ecosystems, but disagreement arises with regard to the extent to which other factors, some spatially heterogeneous and complex in nature, are significant in maintaining these systems.

Faced with the reported complexity of tree-grass interaction at the local scale that may define the large-scale savanna vegetation structure [50], is there any hope of meeting the challenge of predicting vegetation response to changing climate in these environments [55]? Do more dominant factors exist that may supersede these locally-specific interactions and promote the persistence and distribution of tree/grass coexistence? The answer to this may be addressed through examining the links between the hydrological cycle and vegetation dynamics, which may be characterized through both observations and modeling at the regional scale. We undertake such an approach, applied to a savanna system in southern Africa, with the following objectives: (1) to infer the controls on grass growth in space and time, (2) to determine the effects of the dynamic grass cover on the overall ecosystem water use, and (3) to explore the reasons why vegetation assemblages with a dynamic growth component may be favorably suited to persist in fluctuating environments. We emphasize that this is a test of the notion that savanna systems tend to self-organize with respect to maximizing water use, despite the fact that selection processes operate at much lower levels.

2. Site description

The setting for the present analysis is the Kalahari transect (KT) in southern Africa, which is one in the global set of International Geosphere-Biosphere Programme (IGBP) transects [30] and is characterized by a north-south decline in mean annual rainfall. This transect has been the site of a number of recent investigations pertaining to vegetation patterns [12,39,48,49], vegetation-atmosphere exchange [35,44], and nutrient

cycling [1,6]. The climate along the KT is seasonal, with a well-defined wet season lasting from October to March. On average, approximately 87% of the annual rainfall is confined to these months for locations along the transect, with the wet season totals ranging from about 1600 mm/yr to 300 mm/yr from the northern to the southern end of the transect (12°–26°S lat.). Although the KT vegetation is comprised of a wide range of species, general trends relating vegetation to climate have nevertheless been observed. Among these are strong, positive correlations linking the long-term rainfall with woody plant basal area and species diversity [49].

A key feature of the KT is the presence of an aeolian sand formation that underlies a large portion of the transect, having depths on the order of tens of meters. The Kalahari sand serves an important role both in the context of remote sensing, by providing relatively uniform background reflectance for spectral analyses, and in terms of isolating the influence of hydrological factors on vegetation structure, since soil texture is known to be a significant modifying parameter [19,21]. The long-term aridity gradient, overlaying this largely homogeneous substrate, provides an ideal natural setting in which to relate vegetation and climate, and serves as a space-for-time substitution in examining vegetation response to longer-term climate shifts.

A map of the interannual variance in mean wet season NDVI(σ^2_{NDVI}) for the years 1983–1998 is shown in Fig. 1, along with a profile of the mean wet season rainfall along the transect. The peak in the temporal variance in NDVI occurs in central Botswana and corresponds to an area that receives intermediate wet season rainfall totals. This peak in σ^2_{NDVI} cannot be attributed to a co-located high variability in wet season rainfall, since rainfall variability peaks in the northern section of the KT, in the countries of Angola and Zambia (data not shown). Instead, the σ^2_{NDVI} peak in central Botswana is the result of a greater *sensitivity* of the NDVI to variability in wet season rainfall, an attribute
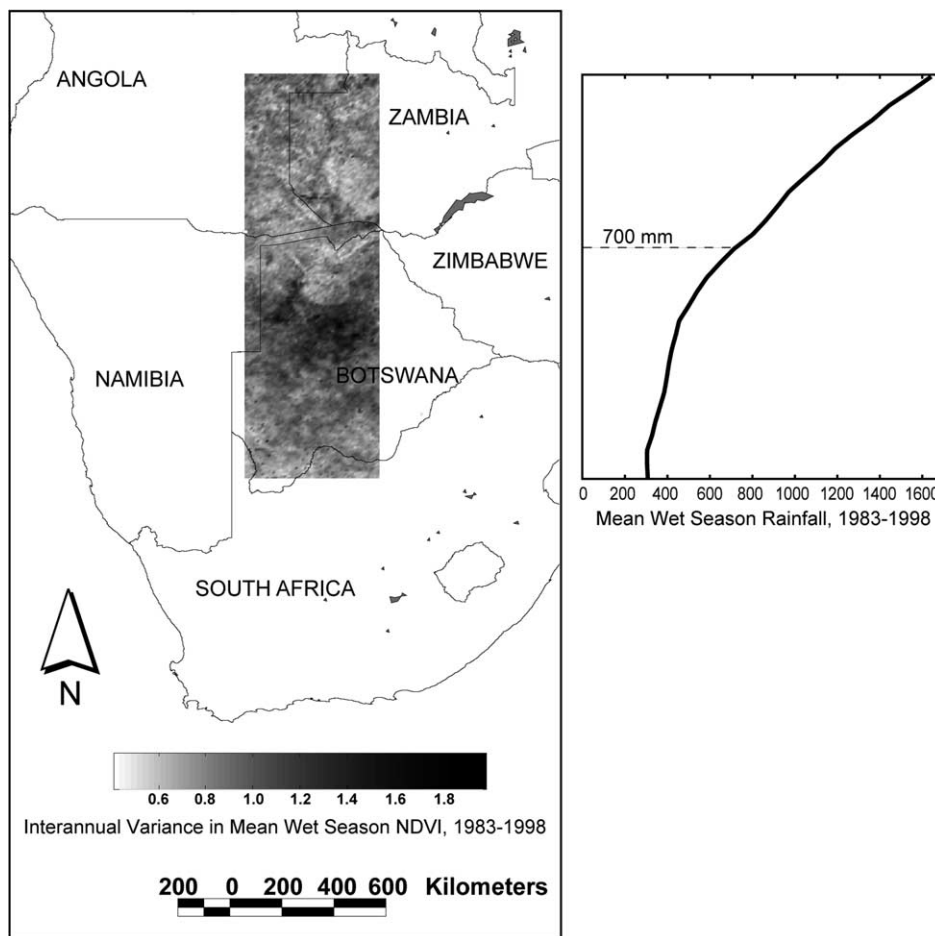

Fig. 1. Map of the interannual variance in mean wet season normalized difference vegetation index (NDVI) for years 1983–1998, as measured by NOAA-AVHRR satellites. The Kalahari Transect (KT) is characterized by an aridity gradient (see inset), with a mean wet season rainfall of 700 mm representing the approximate dividing line between nutrient and water limitations on vegetation growth, as inferred from vegetation physiognomy observations and modeling results. The peak in NDVI variance found in central Botswana is a reflection of the dynamic grass cover, which resonates with wet season rainfall in this water-limited portion of the transect.

that has been used as a basis for vegetation classification [46], in which grass fractional cover is identified as the component of savanna vegetation whose growth is more highly sensitive to fluctuations in rainfall.

By combining the satellite-derived ground cover with a hydrological model, [45] found that the KT vegetation was divided into two distinct zones of limitation: (1) water limitation for the arid portions of the KT with mean wet season rainfall, $\bar{r}$, less than approximately 700 mm/yr and (2) an inferred nutrient limitation for $\bar{r}$ greater than this amount. This agreed well with an independent classification scheme [49,51], in which the dividing line between nutrient-rich, fine-leafed savannas and nutrient-poor, broad-leafed savannas corresponded to roughly the same threshold of $\bar{r}$. Since the focus of this paper is on water-limited vegetation, we examine the portion of the KT where $\bar{r} < 700$ mm/yr, and the dynamical aspect of the vegetation is most pronounced.

3. Methods

The approach presented here is a natural extension of earlier, analytical work that assumed static rainfall and vegetation [17,18], and variable rainfall and static vegetation [31,37,40]. Incorporating dynamic vegetation into a model driven by stochastic rainfall adds another level of complexity and therefore requires a numerical approach. The hydrological model used in this study follows the mathematical framework and parameterization of [45], in which simulations were undertaken for equally-spaced positions along the KT rainfall gradient based on 16 years of climatic measurements and satellite-derived ground cover information (1983–1998) as input. Results from the hydrological model were compared with short-term eddy covariance flux data measured at multiple sites along the KT [45]. The present implementation differs from this earlier work in that the grass fractional cover, x_g, is not assigned a priori for each model simulation but is instead allowed to evolve throughout each wet season according to a growth/decay equation that is governed by the soil moisture in the near-surface soil layer.

The two-layer soil moisture model tracks the time-varying volumetric moisture in a near-surface upper layer, θ_1, and in a deeper layer, θ_2, with grass evapotranspiration (ET_g) influenced by θ_1 and tree evapotranspiration (ET_t) by θ_{tot}, which is the depth-weighted mean of θ_1 and θ_2. Tree fractional cover, x_t, for a particular location along the KT is assigned as its satellite-observed value according to the method of [46] and is assumed not to change over the course of the 16-year simulation. The remainder of the fractional cover is dynamic, converting between either x_g or bare soil, x_b, depending upon wet season moisture availability. The fractional cover of the vegetation components,

which sum to unity, weight the amount of moisture that is removed via evaporation/evapotranspiration from their associated soil layers. Reduction of the soil moisture below a limiting value results in evapotranspiration that is less than the potential rate, and causes stress to the vegetation. Stress for trees and grass, ξ_t and ξ_g, respectively, is quantified according to:

$$\xi_t = \begin{cases} \left[\frac{\theta_t^* - \theta_{tot}}{\theta_t^* - \theta_{wilt,t}}\right]^q & \theta_{tot} < \theta_t^* \\ 0 & \text{otherwise} \end{cases}$$

$$\xi_g = \begin{cases} \left[\frac{\theta_g^* - \theta_1}{\theta_g^* - \theta_{wilt,g}}\right]^q & \theta_1 < \theta_g^* \\ 0 & \text{otherwise} \end{cases} \tag{1a, b}$$

after [41,42], where θ^* is the value below which soil moisture becomes limiting on transpiration and θ_{wilt} is the wilting point, both of which are specific to the tree (subscript t) and grass (subscript g) functional types. The parameter q is used to describe the degree of non-linearity in the soil moisture-stress relationship. The soil moisture model tracks the vertical movement of water through the soil, with the flux of water from the upper to lower soil layers (which can be negative or positive) represented by L_1, and the amount of water that is lost from the base of the deep root zone specified as q_{loss}.

The model was developed in such a way as to maximize the use of available data as input, while keeping parameterization at a minimum. As described in further detail in [45], longwave and shortwave radiation components used to model potential evapotranspiration were taken from satellite observations [15], while wet season daily rainfall time series along the KT were generated according to a stochastic process that assumed an exponential distribution of rainfall depths and random storm arrivals at a given frequency [46]. The stochastic daily rainfall model was driven by rain gauge data that were collected at a number of meteorological stations in the Kalahari region [36]. Soil parameters were assigned based upon empirical relationships for the sandy soil classification [13], and the vegetation parameters (i.e. $\theta_{wilt,t}$, $\theta_{wilt,g}$, θ_t^*, θ_g^*) were based on those measured at another southern African savanna field site having similar sandy soils [51]. Parameter values used in the model are listed in Table 1.

The aspect of the model that requires calibration is the formulation associated with the fractional (green) grass cover. This is determined by the model according to the expression:

$$\frac{dx_g}{dt} = ET_g \chi (1 - x_t) - \xi_g \eta x_g \tag{2}$$

where t is time, χ is analogous to a water use efficiency that converts the water lost via transpiration/photosynthesis into a commensurate gain in the grass fractional cover, $(1 - x_t)$ is used to account for the competitive exclusion of grass fractional cover by the presence of

Table 1
List of parameters used in the simulations

Parameter	Description	Value	Source
θ_t^*	Limiting soil moisture, trees	0.17	Scholes and Walker [51]
θ_g^*	Limiting soil moisture, grass	0.12	Scholes and Walker [51]
$\theta_{\text{wilt,t}}$	Wilting point, trees	0.065	Scholes and Walker [51]
$\theta_{\text{wilt,g}}$	Wilting point, grass	0.040	Scholes and Walker [51]
S_t	Interception store, trees	0.002 m	Scholes and Walker [51]
S_g	Interception store, grass	0.001 m	Scholes and Walker [51]
n	Porosity	0.40	Clapp and Hornberger [13]
K_{sat}	Saturated hydraulic conductivity	2000 mm day^{-1}	Clapp and Hornberger [13]
B	Soil hydraulic parameter	4.05	Clapp and Hornberger [13]
d_1	Depth of upper layer	0.20 m	Estimate from observations
d_2	Depth of lower layer	1.50 m	Estimate from observations
q	Vegetation stress parameter	2	Rodriguez-Iturbe et al. [41,42]

trees, and η is used to translate the grass stress into a coefficient of mortality. The term x_g shows up in the formulation for ET_g [45] as a weight on Priestly-Taylor [38] evapotranspiration such that it is specific to the grass fractional cover component. More complex equations for grass vegetation growth exist [34], but (2) has the benefit of not requiring extensive parameterization while maintaining a form necessary to capture the grass growth/decay in a physically meaningful manner. In the model implementation, x_g evolves on a daily time step and is compared with the fractional grass cover observed by satellites during the January/February/March (JFM) portion of the wet seasons. The parameters χ and η are adjusted in order to match the model output with the remote sensing observations. Initial grass cover conditions for the start of each new wet season were seeded according to $x_g = 0.01(1 - x_t)$. The seeding coefficient was primarily responsible for affecting the grass cover during the early portion of the wet season.

The daily model is applied over a timeframe of 16 wet seasons, at equally-spaced intervals along the KT for the section that receives less than 700 mm of mean wet season rainfall. In order to explore the role of the dynamic grass cover in terms of the savanna water use, the case in which the grass cover dynamics are governed by Eq. (2) is compared with a case in which x_g is static and set to the 16-year average. Specifically, this comparison is evaluated with regard to two quantities which we believe to be fundamental to the water-limited savanna system:

(1) Σq_{loss}, the total amount of water that is lost from the base of the root zone and thereby goes unexploited by the savanna vegetation, and
(2) $\Sigma \xi_t$, the total tree stress relative to a minimal threshold needed to promote tree growth and survival.

Both of these quantities are summed over all of the days of the wet season. The first point tests a global metric, concerning how fully the overall savanna vegetation uses the limiting resource. The second point is specific to the tree cover, which requires a sufficient supply of water to be available for uptake by the relatively inadaptable woody structure and extensive root system. This is in contrast to grass cover, the perennial extent of which adapts to the transient state of available soil moisture. The above conditions demand a tenuous balance between the water cycle and vegetation composition at the land surface for maximal use of the limiting resource. Tree cover should be dense enough to fully utilize the water that reaches the deeper soil layer, but not too dense as to induce stress by removing too much of this water. Year-to-year variability in wet season rainfall, along with the role of dynamic grass cover, is a focus in our evaluation of this balance.

4. Results

Simulations were performed at each of the 111 positions along the KT at daily time steps for 16 years, corresponding to the timeframe of available data from 1983 to 1998. Tree fractional cover, x_t, at each of these positions was set to its satellite-derived value based on the method of [46], which was shown to produce good agreement with field measurements. Fig. 2 shows x_t as a function of mean wet season rainfall along the portion of the KT where $\bar{r} < 700$ mm/yr. These independently-derived data exhibit a strong correlation, with 94% of the variance in x_t explained by $\bar{r}$. The projected grass fractional cover, x_g, likewise derived from the time series of remote sensing data, shows a much different pattern with respect to $\bar{r}$ (Fig. 3a). Notably, there is high variability in x_g at each position along the KT, since the green grass biomass is highly sensitive to the amount of rainfall received during a given year. The envelope of the variability in x_g reaches its smallest extent at the wettest and driest portions of the transect, and peaks at an intermediate mean wet season rainfall corresponding to an value $\bar{r}$ of approximately 440 mm/yr. The 16-year mean in the satellite-derived x_g also exhibits a subtle peak around this middle section of the transect.
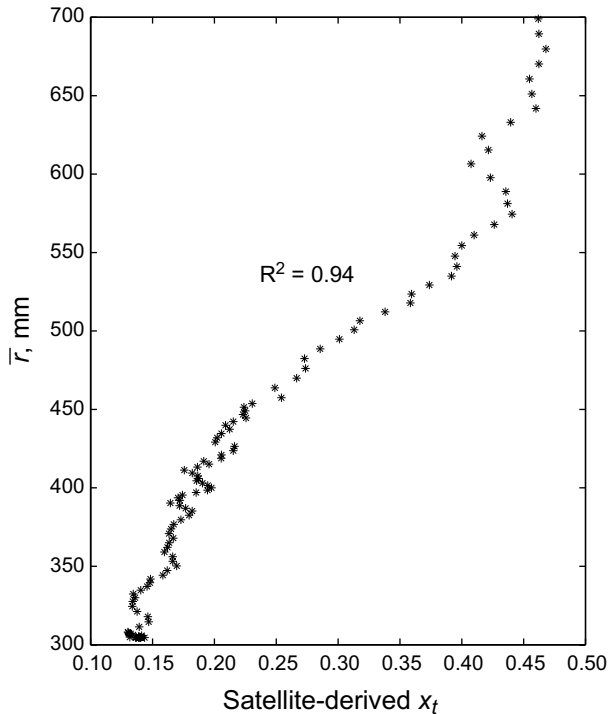
Fig. 2. Satellite-derived fractional tree cover, x_t, varies in relation to mean wet season rainfall, $\bar{r}$ for the water-limited portion of the KT. Approximately 94% of the variance in x_t is explained by the independent variable $\bar{r}$, which was interpolated from long-term rainfall records at meteorological stations along the KT [36].

The empirical parameters χ and η in the model were adjusted in an effort to match satellite-derived observations of x_g, in terms of its mean, variance, and range for the entirety of the KT. Visual inspection was used as the basis for this evaluation, since we were not able to decide upon a robust quantitative measure that would satisfactorily track these three equally important criteria while providing a goodness of fit that would balance the entirety of the transect. Global values of 0.014 day mm^{-1} for χ and 0.50 for η were eventually settled upon, and the model results for the yearly extents of x_g are presented in Fig. 3b.

As a basis for determining the hydrological function of the variable grass cover, we compared the model results generated by dynamic and static grass cover cases. For the latter scenario, x_g was held to its mean value at all positions along the transect (corresponding to the dashed line in Fig. 3b) for each of the 16 years of simulation. In evaluating the results from dynamic vs. static model cases, we find that the dynamic grass cover plays the dual beneficial roles of reducing total tree stress (Fig. 4a) and, in most cases, reducing the amount of water that is lost from the overall root zone (Fig. 4b) relative to the static case. During dry years, the reduced grass cover allows more infiltrated rainfall to reach the deeper soil layers, since less water is lost as transpiration from the upper layer. During wet years, the more expansive

dynamic grass cover generally means a reduction in the amount of water that flows downward into to the deeper soil layer, an excess of which can eventually be lost from the base of the root zone. In some years, the static grass cover does a better job of reducing the amount of water that is "wasted" as Σq_{loss} by this water-limited ecosystem, but it is quite clear from the center of mass in the points in Fig. 4b that the dynamic grass cover is generally more efficient in this regard.

As alluded to in the above description, the dynamic nature of the grass can be thought of as reducing the temporal variance in the interannual values of ΣL_1, the amount of water that moves vertically from the upper to lower soil layers during a wet season. Reduced variance in ΣL_1 leads to more constant recharge to the deeper soil layer, ideally of an amount that is sufficient to allow the trees to maintain maximum productivity (i.e. minimal stress), yet not so much as to allow water to drain from the root zone and go unexploited by the vegetation. Of course, the optimal amount of ΣL_1 needed to strike this balance depends upon tree density. For instance, drainage to the lower root zone layer totaling $\Sigma L_1 = 200$ mm over a wet season may be sufficient for sparse tree cover, resulting in minimal $\Sigma \xi_t$, but this same amount would not satisfy the demand of a more dense tree cover and would result in high $\Sigma \xi_t$. The ideal drainage to the deeper layer over a wet season would be approximated as the amount required to increase the soil moisture from its initial value at the start of the wet season (estimated as midway between $\theta_{t,wilt}$ and θ_t^*) to the level at which soil moisture does not limit transpiration (θ_t^*), plus an amount equivalent to the total unstressed tree evapotranspiration for the wet season. This latter portion is estimated using a Priestley-Taylor formula for potential evapotranspiration, weighted by the fractional tree cover, x_t, and the fraction of the tree root zone that occupies the deeper layer, $(d_2 - d_1)/d_2$. This total amount of water required to satisfy the potential water demand of the trees from the deep soil layer, $\Psi(x_t)$, is evaluated with respect to the modeled drainage to this layer, ΣL_1.

Fig. 5a shows the histogram of $\Sigma L_1 - \Psi(x_t)$ that was generated from all of the model runs along the transect. A clearly-defined range of $\Sigma L_1 - \Psi(x_t)$ exists in which Σq_{loss} and $\Sigma \xi_t$ are minimal (Fig. 5b), a condition that promotes optimal water use by the vegetation. The peak in the $\Sigma L_1 - \Psi(x_t)$ histogram falls within this optimal range, more evidence that the tree density is highly tied to the mean water availability. The adaptable, dynamic nature of grass cover growth reduces the year-to-year variability in ΣL_1, acting as a buffer against variability in wet season rainfall. This narrows the distribution of $L_1 - \Psi(x_t)$ around its first moment (16.3 mm), which corresponds to the general location at which Σq_{loss} and $\Sigma \xi_t$ are minimal (Fig. 5b). The dynamic aspect of grass cover is significant for closing the surface water balance
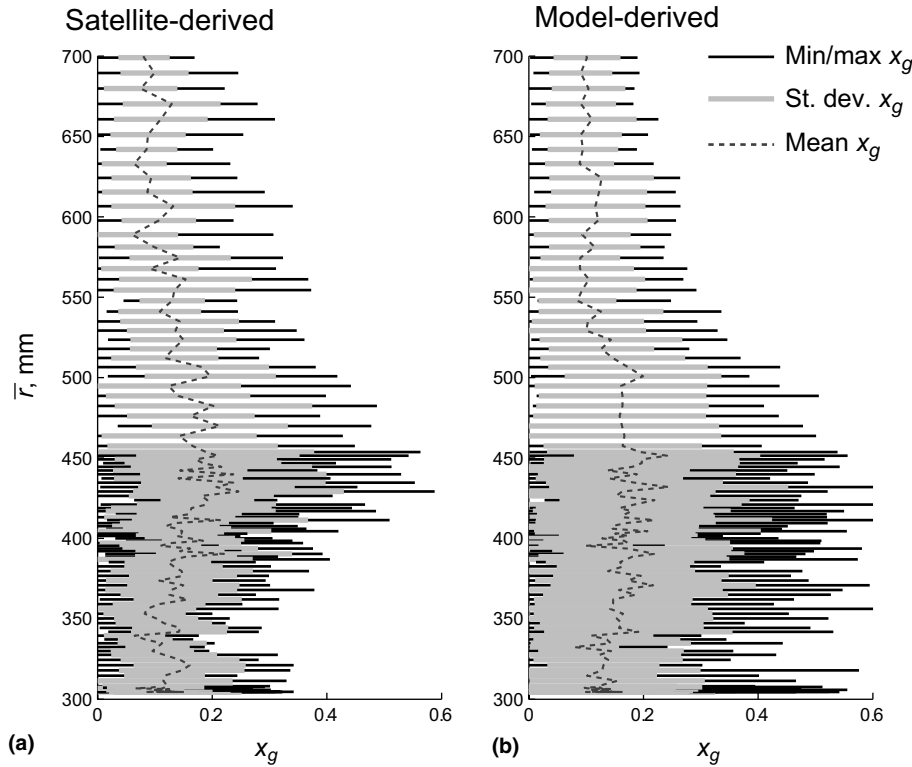
Fig. 3. Temporal mean, standard deviation, and range of fractional grass cover, x_g, with respect to the mean wet season rainfall, $\bar{r}$, at each position along the water-limited portion of the KT during the timeframe 1983–1998. Shown here are (a) satellite-derived x_g from the method of [46], and (b) modeled x_g. Annual values of x_g are taken to be the average fractional grass cover during January–March, the last three months of the wet season. The non-linear relationship between $\bar{r}$ and latitudinal position along the transect makes the spacing of the data non-constant over the y-axis.

(i.e. minimizing Σq_{loss}) and protecting the trees against water stress (i.e. minimizing $\Sigma \xi_t$).

5. Discussion

The overarching control of hydrological factors on the savanna structure is apparent from the substantial correlation between mean wet season rainfall and tree fractional cover shown in Fig. 2, a finding that is consistent with relationships drawn from field data [49]. Fire, browsing, and herbivory are no doubt important modifiers to the savanna structure, especially at the local scale, but their respective influences are hardly sufficient to explain the large-scale patterns of vegetation composition along the KT. Expressed alternatively, the north-south gradient in x_t is not due to a similar gradient in any of these other factors. For instance, fire, which acts as a hindrance to woody vegetation establishment, is much more prevalent in the northern portions of the transect [10] where tree cover is most dense. Although such data are not readily available, it is reasonable to assume that browser or grazer populations gradients are also not coincident with the north-south decline in tree cover.

A more nuanced argument for the significance of these disturbance factors would posit that, while rainfall is the key variable in defining the vegetation biomass along the KT, one or more of these disturbance factors must prevail in modifying the vegetation such that it reaches a mixed compositional form. Underlying this is an assumption that vegetation will tend toward a climax state that is characterized by minimal structural diversity (i.e. uniformity) [26]. While such an argument is probably rooted in classical succession theory, an alternative view is that these savanna systems will tend toward a compositional organization that will maximize the use of the limiting resource, in this case water, and that disturbance drives the system away from this configuration. The degree to which the present vegetation structure is optimized with regard to water use for the largely undisturbed KT savanna system is revealed through the model analysis.

While fractional tree cover is closely related to $\bar{r}$, the fractional grass cover is highly tied to fluctuations in wet season rainfall and the existing x_t. The interesting pattern in the observed x_g data presented in Fig. 3a shows a limitation on grass growth in the wettest and driest regions of the transect, features that can likely be explained by terms in Eq. (2). Tree cover limits x_g in the
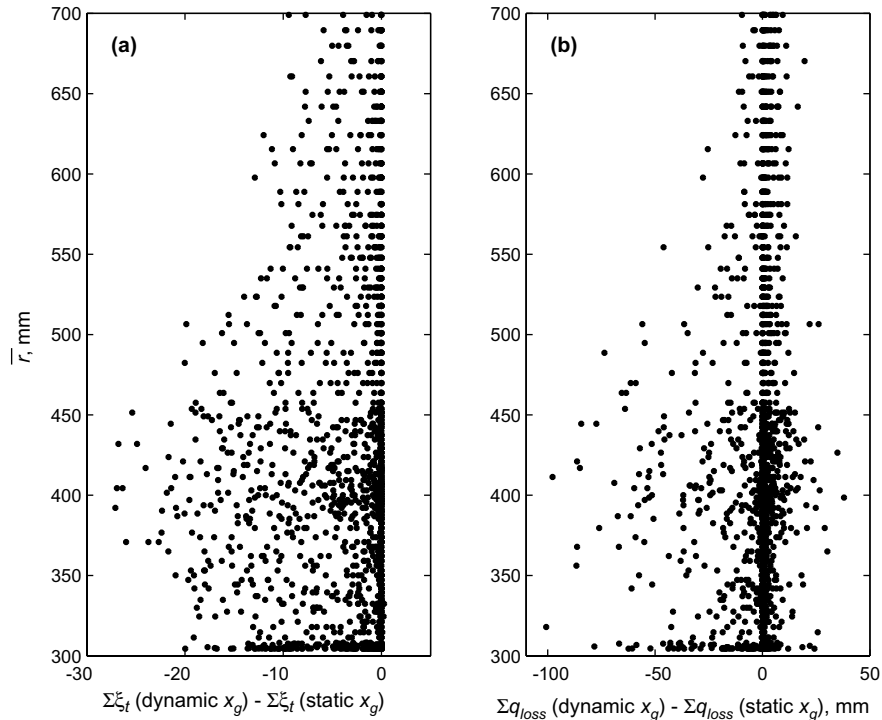
Fig. 4. Comparison of the model results for dynamic grass cover, which evolves according to Eq. (2), and static grass cover, which was set to its 16-year mean value at each location. The dynamic grass cover generally resulted in (a) lower total tree stress, $\Sigma\xi_t$, and (b) lower amounts of water lost from the base of the root zone, Σq_{loss}, at each location along the transect characterized by mean wet season rainfall, $\bar{r}$, for the suite of the 16-year simulations.
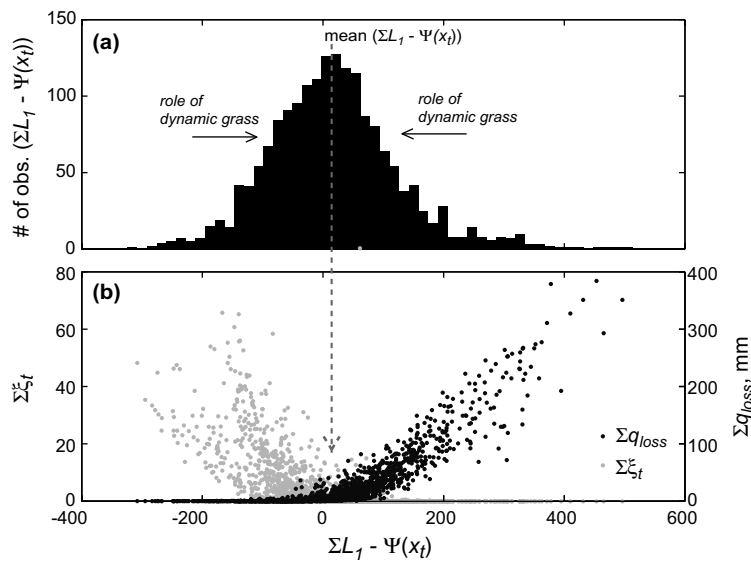

Fig. 5. Model results for each of the 16 years at all positions along the transect. (a) Histogram of $\Sigma L_1 - \Psi(x_t)$, the difference between the amount of water that drains from the upper to the deeper soil layer and amount that is ideal for tree use from this zone. The dynamic grass cover reduces the variance in ΣL_1, supplying the deeper soil horizon with a more constant annual replenishment of water. (b) Model results for the entire transect show that there small range of $\Sigma L_1 - \Psi(x_t)$ over which both $\Sigma\xi_t$ and Σq_{loss} are minimized, a condition that infers optimal vegetation water use.

wettest region of the transect, as accounted for by the $(1 - x_t)$ term in the modeled growth. Since satellites monitor the projected cover, meaning that the overhead view angle does not allow grass that is below the tree canopy to be detected, this term is needed to determine probabilistically the growth that occurs only in the area between the tree canopies. The $(1 - x_t)$ term can also be thought of as a light limitation on the grass growth that

is imposed by the existing tree canopy cover. In the driest section of the transect, the limitation is probably caused by the low rainfall totals that are experienced in this region. The model tends to overpredict x_g at the dry end of the transect (Fig. 3b), which might be due to choice of the stress parameter, ξ_g, instead of a more complex alternative that could factor in the duration of the soil moisture excursions below the limiting value [37]. Nevertheless, the simple equation that is solely based on tree cover and near-surface soil moisture does a reasonable job of reproducing the observed extent of the grass fractional cover through space and time along the KT.

During dry years, the reduced extent of the grass cover has a facilitative effect on tree water use, in that more water (compared to the static x_g case) is allowed to drain to deeper depths, thereby reducing the tree stress (Fig. 4a). For wet years, a greater amount of water is usually removed from the upper soil layers by the dynamic grass cover, and therefore less water eventually drains from the base of the overall root zone (Fig. 4b). The dynamic grass cover helps close the tenuous water balance at the land surface by resonating with the high-frequency (i.e. subannual to annual) variability in rainfall. In a given wet season, the total amount of water that reaches the deep soil layer (ΣL_1) should be enough to allow tree transpiration and carbon assimilation to proceed at a maximum rate (e.g. minimal $\Sigma \xi_t$), yet not be too much as to allow this limiting resource to be wasted (e.g. minimal Σq_{loss}). In order for the ecosystem water use to be most efficient, the wet season ΣL_1 should be constant, specific to the tree density at a given location. This would be an idealized situation, of course, whereas in reality there is variability in wet season ΣL_1, causing tree stress during very dry years and leakage losses during very wet years. What the dynamic grass cover does, however, is to reduce the variance in ΣL_1, thereby buffering the effects of climatic variability on the ecosystem water use.

In evaluating the model results for the entire transect, we needed to account for the fact that the tree cover varies along the rainfall gradient. Therefore, in determining if the modeled ΣL_1 was suitable for maximizing water use at each of the respective positions along the transect, we used the expression $\Sigma L_1 - \Psi(x_t)$ as the independent variable in Fig. 5. By our doing so, the surface that defines the ecosystem water use became well-defined (Fig. 5b), and it also became apparent that vegetation composition along the KT is organized with respect to the dual water-use considerations, as evidenced by the position of the $\Sigma L_1 - \Psi(x_t)$ histogram peak (Fig. 5a). The dynamic nature of the grass cover in response to variable rainfall enhances the degree to which the savanna ecosystem maximizes water use and helps close the water cycle at the land surface.

Calibration was undertaken only for χ and η, which were adjusted in order to match the model output with the satellite observations (Fig. 2). All of the other model input and parameters were assigned based on satellite or ground-based observations or best estimates from field data [45], and no further tuning took place. Even so, it is worthwhile to speculate as to how robust these finding are with respect to model parameterization or conceptual design. In particular, how do the a priori root zone niche designations for trees and grass affect the conclusions drawn from this study? To answer this, consider the extreme case in which the tree/grass root zone niche overlap is complete. For this scenario, it is still apparent that the positive correlation between soil moisture and grass fractional cover would work to decrease the temporal variance in soil moisture, thereby promoting unstressed tree evapotranspiration during dry years, while boosting the overall ecosystem water use during wet years. The competition between trees and grass for soil moisture would be altered in this case, but the qualitative findings would be similar. Another potential criticism of the model presented here is the fact that it is not spatially explicit in the horizontal domain. Indeed, other studies have used horizontal interactions as the basis for modeling tree/grass coexistence [11,27,28]. In modeling the soil moisture, the use of a strictly vertical discretization can perhaps be justified by the fact that tree root profiles extend outward at depth into the inter-canopy space, and horizontal gradients in soil moisture tend to diminish relatively quickly through time in these sandy soils. The horizontal vs. vertical spatial variance in soil moisture specific to the savanna vegetation mosaic is an aspect that we hope to characterize better in the future. Finally, the parameterization of this large-scale model is simplified, in that we assign vegetation water use parameters by functional type rather than accounting for the species-specific variability that is undoubtedly present in the natural system. Despite this simplification due to the lack of available data, we submit that the impact on the modeled hydrological dynamics provided by the variable grass cover is much more significant than that imposed by potential inaccuracies in the assigned vegetation parameters.

From a water use perspective, a pure grassland or woodland situated in the KT environment would be less efficient than the existing mixed tree/grass savanna in terms of exploiting this limiting resource. The shallow root system of grasses, combined with the sandy soils and the exponential distribution of storm rainfall depths, would allow significant amounts of water to bypass the root zone of grassland vegetation. Even though the absence of trees would allow the green grass biomass to be extraordinarily responsive to the rainfall in terms of growth, this would not make up for the decreased efficiency in water use imposed by the uniformly shallow root depth. In the case of a woodland ecosystem, the water use of the standing biomass would be constrained by the woody structure, making the ecosystem water use

less adaptable to fluctuations in wet season rainfall. Tree density in such a system would have to be conditioned upon the mean wet season rainfall, but this would mean that $\Sigma\xi_t$ would be greater during dry years and Σq_{loss} would be greater in wet years in the absence of the grass cover to buffer the effects of rainfall variability. Ideal mono-specific vegetation for this climate and soil type would have the joint attributes of (1) non-definite lateral growth that is highly responsive to soil moisture, and (2) a deeply penetrating root system. No vegetation of this type exists, but the tree/grass mixture of a savanna eco-system does, in a collective sense, have the benefit of possessing both qualities. This is an example of in-creased ecosystem robustness arising from the complex, adaptive nature of vegetation assemblages [33].

The model results indicate that as the savanna com-position moves toward a grassland through tree thin-ning [53] or toward a woodland through excessive grazing [2], the efficiency of the surface water balance closure will be reduced, leading to greater recharge rates. Recent findings by [58] in the arid southwestern United States showed that large reservoirs of nitrate have built up in the soil below the root zone as a result of many years of leaching. If the same is true for the Kalahari soils, then increased recharge could mobilize the nitrate and possibly contaminate the groundwater supply. Understanding the role of the dynamic vegetation in influencing the water balance at the land surface is key to this and many other issues in semi-arid environments, since the hydrological biogeochemical cycles are so clo-sely linked at the land surface.

6. Conclusions

Vertical root zone niche separation for trees and grasses has commonly been perceived as the defining factor that differentiates water use by these two compo-nents of savanna vegetation, but we find that the con-trasting timescales of growth associated with their respective fractional covers is also an important distinc-tion in terms of water use. For the uniform sandy soils of the KT, observations reveal that tree density is highly dependent upon the long-term mean of wet season rain-fall, while grass fractional cover is variable on an annual basis with its extent primarily governed by both the availability of near-surface soil moisture and the density of the existing tree cover. In the frequency domain, the tree cover along the KT would be hypothesized to re-spond to low-frequency variability in rainfall (i.e. deca-dal timescales), while grass cover would respond to high frequency variability in rainfall (through θ_1) as well as low-frequency variability (passively through $(1 - x_t)$).

High variability of annual rainfall is not unique to this region of the world, but in this water-limited arid envi-ronment this aspect does become important in terms of

shaping vegetation form. As end-members in the savanna vegetation spectrum, pure grasslands or woodlands would not fully maximize use of this fluctuating resource in the KT due the grass's shallow root depth and the tree's rigid, woody structure that does not allow for adaptable lateral growth. Water use by mixed compositional savan-nas, on the other hand, benefits from both the dynamic nature of grass cover and the deep root zones of trees. Model results show that the savanna vegetation along the KT is organized with respect to maximizing water use in this environment that is subject to variable rainfall. Specifics about the tree-grass interactions and distur-bance effects through stages of growth that give rise to such compositional arrangements are not addressed in this study, but research along these lines has been under-taken [9,20,24,29,59] and more is needed. Based on obser-vational and modeling evidence, this study points to a dynamic equilibrium configuration towards which the savanna system tends to become organized.

Acknowledgments

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