

ECOHYDROLOGICAL OPTIMIZATION OF PATTERN AND PROCESSES IN WATER-LIMITED ECOSYSTEMS

KELLY K. CAYLOR,¹ TODD M. SCANLON,² IGNACIO RODRÍGUEZ-ITURBE³

1. INTRODUCTION

The coupled nature of hydrological and ecological dynamics is perhaps nowhere more evident than in semi-arid ecosystems. Frequently stressed and sensitive to change (Guenther *et al.*, 1996), semi-arid ecosystems are responsive to climate variability over relatively short time scales, and water is the main driving force in shaping the vegetation distribution and composition (Rodríguez-Iturbe *et al.*, 1999; Smit and Rethman, 2000). The dynamical nature of the vegetation response to water availability is a prominent feature of semi-arid ecosystem function, as is evident from satellite observations (Goward and Prince, 1995; Scanlon *et al.*, 2002). Despite the close coupling that exists between water and vegetation structure, the challenge of predicting vegetation response to changing climate in these environments is particularly daunting (Daly *et al.*, 2000). Specifically, a central challenge is defining the ecologically and hydrologically relevant processes that led to the formation of vegetation patterns in water-limited ecosystems.

The complex interactions between plants, soils, and climates in semi-arid ecosystems make it difficult to define specific ecohydrological optimization mechanisms that underlie observed landscape-scale patterns in vegetation structure. Regional models of semi-arid vegetation structure are often biogeographical in nature, making predictions based exclusively on the role of external factors such as mean annual rainfall, or soil infertility imposed by geologic constraints. These kinds of relationships often yield reasonable predictions of savanna ecosystem structure (Sankaran *et al.*, 2005; Huxman *et al.*, 2005), but provide little additional insight in the specific ecohydrological processes that maintain vegetation-climate co-organization. At the scale of plant canopies, it has also been recognized that the role of vegetation itself

¹ Indiana University, Department of Geography.

² University of Virginia, Department of Environmental Sciences.

³ Princeton University, Department of Civil and Environmental Engineering.

on resource availability can be critical in semi-arid ecosystems (Archer *et al.*, 1988). Indeed, the strong control that individual plants can exert on local water balance has recently been highlighted by the field observations of Seyfried *et al.* (2005) and Ludwig *et al.* (2005) who demonstrate variation in surface moisture redistribution caused by the mosaic of vegetation patches and inter-patch areas in a variety of semi-arid ecosystems. The conceptual models arising from these field-scale studies explicitly couple biological pattern to abiotic factors; usually driven by soil moisture, but often also thought to be determined by nutrients, herbivory, or fire. Based on these considerations, more recent models of savanna structure have taken the small-scale spatial structure of semi-arid ecosystems into account (Jeltsch *et al.*, 1999).

There remains a need to clarify the manner by which vegetation self-organizes across scales within semi-arid landscapes, and how regional, landscape, and individual-based patterns of vegetation interact with their accompanying climates and soils. Such clarification necessitates the development of conceptual models capable of interpreting and predicting spatial pattern formation in savannas (and similar dry woodland ecosystems) as well as metrics for assessing optimization or organization of patterns as one scales from individual canopies to landscapes and beyond.

Here we highlight some recent efforts to link the surface hydrological cycle to the dynamics of vegetation pattern, which we have characterized through both observations and modeling across a suite of semi-arid ecosystems. We emphasize that the results presented here are an exploration of the general hypothesis that many semi-arid ecosystems tend to self-organize with respect to optimizing water use. In our view, a key difficulty arises in assessing which metrics of optimization are relevant at different spatial and temporal scales of interest. For instance, are there generalities of optimization regarding water use that exist across ecosystems? If so, do signatures of 'ecological fitness' leave hydrological fingerprints at the landscape scale? These questions lie at the heart of the emerging science of ecohydrology, and it is our hope that the following discussion demonstrates the utility in viewing semi-arid landscapes through the perspective of ecohydrological organization.

In the current discussion, we focus on the spatial aspects of interactions between plants, soils, and climates in two different water-limited systems. The first is a series of savanna sites spanning a large rainfall gradient within southern African, and the second is a semi-arid river basin organized around a drainage network in central New Mexico. We address these questions at a hierarchy of scales that range from climate gradients spanning thousands of kilometers to that of individual tree canopies spanning only a few meters.

2. REGIONAL PATTERNS OF OPTIMAL WATER USE MEDIATED BY VEGETATION DYNAMICS

Many water-limited ecosystems exhibit dynamic vegetation components whose annual extent resonates with wet season rainfall. A particularly compelling example is the case of dynamic grass vegetation cover determined by regional satellite observations of normalized difference vegetation index (NDVI) time series for the Kalahari Transect in southern Africa. The Kalahari Transect is one of a number of IGBP transects designated throughout the world (Koch *et al.*, 1995) and covers a latitudinal mean annual rainfall gradient varying from 1000 mm/year in the north to 250 mm/year in the south. Consistency in geomorphology over the entire region – primarily deep Kalahari sands (Thomas and Shaw, 1991) – allows for an analysis of vegetation structure and ecosystem processes relatively independent of soil type. The gradient in mean annual rainfall across the Kalahari Transect sites results in dramatic variation in vegetation structure along the transect (Caylor *et al.*, 2004a; Privette *et al.*, 2004; Scholes *et al.*, 2002).

The overarching control of hydrological factors on savanna vegetation structure across the Kalahari Transect is apparent from the substantial correlation between mean wet season rainfall and tree fractional cover derived from satellite data (Scanlon *et al.*, 2002), a finding that is consistent with relationships drawn from field data (Scholes *et al.*, 2002). However, it is often hypothesized that one or more additional disturbance factors must prevail in modifying the vegetation such that it reaches a mixed compositional form. Underlying this idea is an assumption that vegetation will tend toward a climax state that is characterized by minimal structural diversity (Jeltsch *et al.*, 2000). 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. 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 throughout the Kalahari.

Scanlon *et al.* (2005) use the the coupled gradients of vegetation and climate to develop a modeling framework that evaluates the ecohydrological role of observed grass dynamics. Here we demonstrate the use of the model to explore the implications of dynamic grass vegetation on overall ecosystem water use. In particular, we use the model to investigate the degree to which savanna vegetation structure is organized with respect to patterns of region-

al water use and the occurrence of plant water stress. The dynamical simulation of both vegetation and rainfall adopted by Scanlon *et al.* (2005) is a natural extension of earlier, analytical work that assumed static rainfall and vegetation (Eagleson, 1978; Eagleson and Segarra, 1985), and variable rainfall and static vegetation (Laio *et al.*, 2001; Porporato *et al.*, 2001; Rodríguez-Iturbe *et al.*, 2001). The hydrological modeling scheme also builds on the mathematical framework of Scanlon *et al.* (2002), by allowing the fraction of grass cover, x_g , 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. These temporal dynamics of fractional grass cover, x_g are governed by the following equation presented in (Scanlon *et al.*, 2005) as

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

where ET_g represents the transpiration of grasses, χ is a water-use efficiency parameter, and η is a measure of grass mortality associated with the occurrence of grass water stress ξ_g . Calibration is necessary only for χ and η , which are adjusted in order to match the model output with the satellite observations (Fig. 1, see over). All of the other model input and parameters are assigned based on satellite or ground-based observations or best estimates from field data (Scanlon and Albertson, 2003).

The daily model is applied over a timeframe of 16 wet seasons (1983-1998), at equally-spaced intervals along the Kalahari Transect 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 model is used to explore the impact of a dynamic grass cover on two quantities which we believe to be fundamental to the water-limited savanna system. The first is the total amount of water that is lost from the base of the root zone and thereby goes unexploited by the savanna vegetation, which is denoted as Σq_{loss} . The second quantity is the total tree water stress, $\Sigma \xi_t$, which accumulates when the soil moisture within the tree rooting zone drops below a critical value that represents at point of incipient water stress. 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 static woody vegetation cover and its accompanying root system. This is in contrast to grass cover, the extent of which adapts to the transient state of available soil moisture. The above

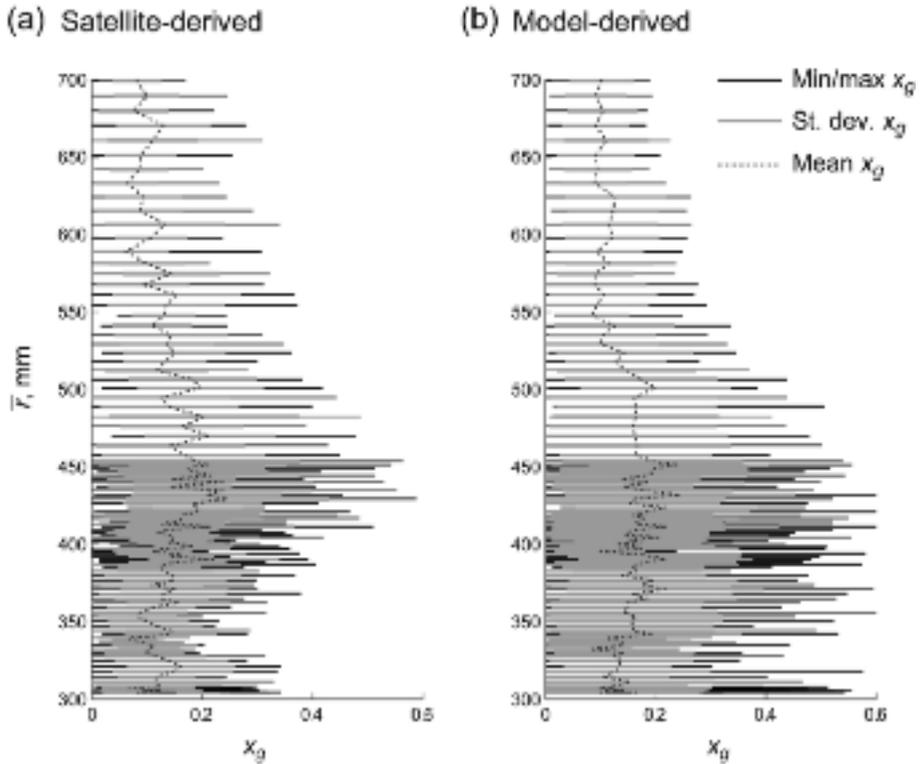


Figure 1. Mean, standard deviation, and range of fractional grass cover, x_g , with respect to the mean wet season rainfall, \bar{r} , for January-March at each position along the water-limited portion of the Kalahari Transect during the timeframe 1983-1998. Shown here are (a) satellite-derived x_g from the method of Scanlon *et al.* (2002), and (b) modeled x_g . The dynamic grass model (Equation 1) shows excellent agreement with the satellite estimates. Figure reproduced with permission from Scanlon *et al.* (2005).

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 water 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.

The results of the model show that during dry years, the reduced extent

of the dynamic grass cover has a facilitative effect on tree productivity, in that more water is allowed to drain to deeper depth than if the grass cover was not dynamically responsive to water availability. This ‘down-regulation’ of grass production in dry seasons thereby reduces the tree water stress. In contrast, for wet years, a greater amount of water is removed from the upper soil layers with the increased dynamic grass cover, and therefore less water is lost from the base of the overall root zone. Therefore the dynamic grass cover helps close the tenuous water balance at the land surface by resonating with the high-frequency (i.e. sub-annual to annual) variability in rainfall. In a given wet season, the amount of water that reaches the deep soil layer is specified as Σ^{L_1} , which represents the total leakage losses from the upper soil layer (the only one the grass has access to). The value of Σ^{L_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 Σ^{L_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 Σ^{L_1} , causing tree water stress during very dry years and leakage losses from the root zone during very wet years. What the dynamic grass cover does, however, is to reduce the variance in Σ^{L_1} , thereby buffering the effects of climatic variability on the ecosystem water use.

An important consideration within the model is the balance between water availability and water use for deeply-rooted woody vegetation across the transect. As rainfall and tree cover increase, we may expect shifts in the amount of vertical percolation (driven by changes in annual rainfall) to deep root layers, as well as shifts in water uptake from these deeper layers (driven by changes in tree cover and potential evapotranspiration). Either supply in excess of demand or demand in excess of supply would indicate a system that was poorly organized for optimal water use. We define the seasonal water availability to deep tree roots as Σ^{L_1} , which is the sum of water that leaves the upper soil layers by percolating downward. The seasonal water availability for the deep tree roots, Σ^{L_1} , should ideally meet the demand of the trees at each position along the regional climate gradient. This demand is determined by the fraction of woody vegetation cover as well as the maximum potential evapotranspiration rate, and is noted here as $\Psi(x_t)$. In evaluating the optimality of vegetation patterns across the entire transect, Scanlon *et al.* (2005) use the expression $\Sigma^{L_1} - \Psi(x_t)$ as an independent variable in Figure 2. This formulation accounts for both the

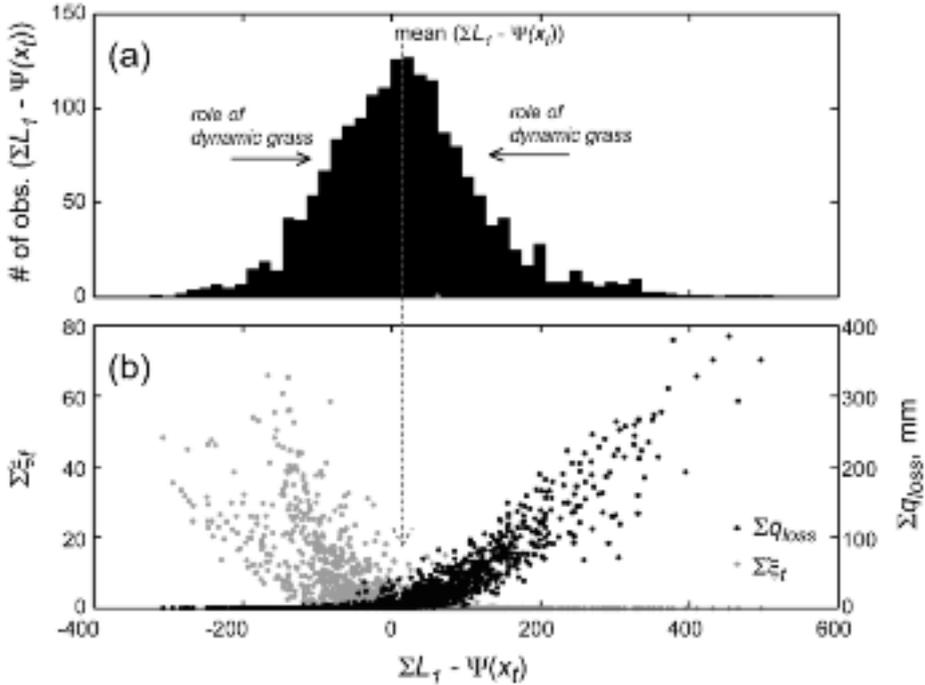


Figure 2. (a) Histogram of $\Sigma L_1 - \Psi(x_t)$, which represents the balance between the supply of water that drains into to the deep soil layer ΣL_1 , minus the demand of water inferred from tree water use $\Psi(x_t)$ at a particular location. The dynamic grass cover reduces the variance in the distribution of supply and demand $\Sigma L_1 - \Psi(x_t)$ and keeps the value close to zero so that there is neither surplus ($\Sigma L_1 \gg \Psi(x_t)$) or deficit ($\Sigma L_1 \ll \Psi(x_t)$). Model results for the entire transect show that the mean value of $\Sigma L_1 \gg \Psi(x_t)$ arising from a dynamic grass layer (a) corresponds to a structural configuration that minimizes both total tree stress ($\Sigma \xi_t$, grey points) and total vertical percolation beyond the rooting zone (Σq_{loss} , black points) (b). Figure reproduced with permission from Scanlon *et al.* (2005).

changing supply and demand for water across the climate gradient. The position of the $\Sigma L_1 - \Psi(x_t)$ histogram peak (Fig. 2a) corresponds to a location of both minimal water loss, Σq_{loss} , and minimal tree water stress, $\Sigma \xi_t$ (Fig. 2b). Since the minimization of these two quantities (Σq_{loss} and $\Sigma \xi_t$) across the transect defines optimal ecosystem water use at each location (Fig. 2b), it is apparent that vegetation composition along the Kalahari Transect is highly organized with respect to these water-use considerations. Therefore, we find that the dynamic nature of the grass cover in response

to variable rainfall enhances the degree to which the savanna ecosystem is optimized with respect to water use and helps to close the water cycle at the land surface.

From a water use perspective, a pure grassland or woodland situated in the Kalahari 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 the woodland ecosystem, the growth 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 tree water stress ($\Sigma \xi_t$) would be greater during dry years and total leakage loss (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 ecosystem does, in a collective sense, have the benefit of possessing both qualities. This is an example of increased ecosystem robustness arising from the complex, adaptive nature of vegetation assemblages (Levin, 1999).

One further conclusion to be taken from the model results of Scanlon *et al.* (2005) is that as the savanna composition moves toward a grassland through tree thinning (Smit and Rethman, 2000) or toward a woodland through excessive grazing (Archer, 1995), the efficiency of the surface water balance closure will be reduced, leading to greater recharge rates. Recent findings by Walvoord *et al.* (2003) in the arid southwestern United States showed that large reservoirs of nitrate have built up in the soil below the root as a result of many years of leaching. Future shifts in the vegetation and climate of these areas could serve to make this nitrate available to plants (i.e. through the establishment of more deeply-rooted species). However, it is also possible that changes in vegetation and climate may enhance vertical leakage such that the nitrate is transported downward to the water table. Regardless, it is clear that understanding the role of the dynamic veg-

etation in influencing the water balance at the land surface is key to this and many other issues in semi-arid environments, since the hydrological and biogeochemical cycles are so closely linked at the land surface.

The model results for this largely undisturbed Kalahari Transect savanna system reveal the degree to which the present vegetation structure appears to be optimized with regard to water use; alternately minimizing water loss in wet seasons and minimizing water stress in dry ones. We note that the use of a two-layer scheme for modeling regional tree/grass water use neglects the potential for horizontal variability in soil moisture and the impacts of such variability on vegetation dynamics. An assumption of horizontal homogeneity may be appropriate for large-scale vegetation/climate modeling. However, more complicated landscapes necessitate a more nuanced view of spatial heterogeneity at the landscape and individual-scale. The final section of this chapter introduces an approach for examining the role of horizontal spatial variance in soil moisture specific to the more localized individual-based savanna vegetation mosaic. However, before turning to these sorts of individual-based patterns, we next explore the landscape-scale dynamics of vegetation within a semi-arid basin of central New Mexico where regional topography plays a crucial role in the climate-soil-vegetation interaction.

3. LANDSCAPE-SCALE ECOHYDROLOGICAL ORGANIZATION OF VEGETATION WITHIN SEMI-ARID RIVER BASINS

While there is a growing awareness of the important role that geomorphology exerts on vegetation structural dynamics and the generation of landscape-scale vegetation patterns in many semi-arid landscapes (Coughenour and Ellis, 1993; Kim and Eltahir, 2004), the question of whether or not the interaction of vegetation, soils, and climate also display a similar set of unifying characteristics among the very different patterns they present in river basins has been relatively unexplored. This is despite the fact that research during the last 10 years has conclusively shown a high degree of organization and unifying principles behind the structure of the drainage network and the 3-dimensional geometry of river basins (Rodríguez-Iturbe and Rinaldo, 1997). The consideration of a river network as a dendritic structure characterized by minimum total energy dissipation (optimal channel networks, or OCNs) has provided a means of connecting the ubiquity of self-affinity and scaling in river net-

works with the physical dynamics of open, dissipative systems. However, it has been shown that in order to reproduce the observed scaling properties of river networks it is necessary to employ suboptimal minimization schemes which restrict their search for optimality to local minima that are accessible from initial conditions. The limitation of natural processes that search for optima which are dynamically accessible within the constraints of initial and boundary conditions has been termed feasible optimality, a condition also observed in systems like Ising ferromagnets (Swift *et al.*, 1997) and the aggregation of metal balls within open, dissipative electrical systems (Marani *et al.*, 1998).

In a series of papers, Caylor *et al.* (2004b), and Caylor *et al.* (2005) consider the argument that minimization of water stress in plants plays a fundamental role in the organization of the vegetation pattern within semi-arid river basins, but that the suite of possible patterns obtained is similarly constrained to a suboptimal configuration due to the limitation of local minima enforced by the structure of the river network. These efforts represent an attempt to integrate more fully the concept of self-organization observed to be present within many patterns of vegetation (Rietkerk *et al.*, 2002; Sole *et al.*, 2002) with the scale-invariance and self-organized complexity known to exist in the geomorphological organization of river basins (Turcotte, 1990; Turcotte and Rundle, 2002; Rodríguez-Iturbe and Rinaldo, 1997). The principles of such organization have important consequences regarding the impact of land cover change on hydrological dynamics in river basins, as well as the geomorphological evolution of landscapes under varying climate and vegetation regimes.

To this end, Caylor *et al.* (2004b) analyze and simulate the spatial distribution of water stress arising from different vegetation configurations in the Upper Rio Salado basin, located near the Sevilleta Long-term Ecological Research (LTER) site in central New Mexico. Using available geospatial data, Caylor *et al.* (2005) assign soil, climate, and vegetation properties across the basin and analyze the probabilistic characteristics of steady-state soil moisture distribution as well as in the distribution of observed vegetation patterns, simulated vegetation dynamic water stress and hydrological fluxes such as transpiration. The seasonal steady-state relative soil moisture probability distribution Laio *et al.* (2001) forms the basis for assessing the plant water stress at each location within the basin. Recent work on stochastic soil moisture dynamics across hillslopes has demonstrated that topography can lead to significant spatial gradients in soil moisture due to lateral soil moisture redistribution, but that such patterns only develop in

relatively humid climates (Ridolfi *et al.*, 2003). Therefore, in this analysis of a semi-arid river basin hillslope dynamics associated with lateral soil moisture distribution are neglected.

To determine the ecohydrological organization of vegetation within the Rio Salado basin, a measure of water stress is adopted from the presentation of Caylor *et al.* (2005). This modified dynamic water stress (Θ') scales the statistical steady state stress condition according to the duration of the mean first passage time between an initial condition associated with the spring snow melt and the statistical steady-state mean. A resulting modified dynamic water stress profile is defined as the average value of the steady-state modified dynamic water stress, $\overline{\Theta'}(x)$, for all points located at the same distance x from the basin outlet measured through the network. Thus,

$$\overline{\Theta'}(x) = \frac{\sum_{i=1}^{N_x} \Theta'_i}{N_x} \quad (2)$$

where N_x is the number of elementary pixels at distance x measured through the drainage network flow path, and Θ'_i is modified dynamic water stress at each of these N_x locations. Therefore, this average modified dynamic water stress is an average quantity conditioned on the network width function, which is itself a well-studied metric of basin geomorphology (Marani *et al.*, 1994) and is derived from our analysis of the USGS digital elevation data described above.

To assess the importance of water stress in determining the distribution of vegetation within semiarid river basins, the existing vegetation pattern of vegetation (Figure 3a, see page 213) is compared to two alternative hypothetical vegetation distributions. The first is the distribution of vegetation that arises from a random assignment of vegetation type at each location within the basin, under the constraint that the proportions of overall land cover composition are preserved over the whole basin (Figure 3b, see page 213). The second hypothetical pattern is the one arising from the specification of the vegetation type that exhibits the lowest dynamic water stress at each location within the basin (Figure 3c, see page 213). From the sole point of view of water stress, the second pattern can be viewed to represent and optimal or ideal distribution of vegetation. A visual comparison of these three patterns (actual, random, and ideal) suggests that the actual pattern of vegetation distribution contains elements of both the highly organized large-scale ideal pattern, as well as the characteristic small-scale variation associated with the random pattern.

The existence of a distribution of water stress globally bounded by the

random and ideal vegetation distribution may allow for the development of dynamic modeling approaches for predicting the distribution of vegetation pattern in river basins under conditions of changing climatic and edaphic regimes. Moreover, it is likely that the vegetation patterns in water-controlled ecosystems tend to approach an optimal configuration in terms of water stress but are subject to important and decisive random contingencies of an altogether different character. Conceptually, this is not different from the notion of feasible optimality at work in the organization of the drainage network (Rigon *et al.*, 1998).

This hypothesis of feasible optimality is explored by Caylor *et al.* (2004b) using two simple cellular automata approaches to model the statistical steady-state conditions of a vegetation mosaic initiated from a random condition (Figure 3, see page 213). Vegetation is initially distributed randomly in equal proportions within the basin (1/3 each of trees, shrub and grass). In both models, the initial random vegetation mosaic is modified through the iteration of local interactions that occur between adjacent locations. These interactions are defined such that vegetation replacement can occur when the stress at a randomly chosen location is less than the stress in an adjacent location. Following the initial random placement of vegetation, a cell at location i within the basin is randomly selected and allowed to replace an adjacent location n with probability $(1 - \Theta'_i / (\Theta'_i + \Theta'_n))$. If a successful replacement occurs, the procedure is repeated with a new neighbor chosen from the locations adjacent to cell n , otherwise a new random location i is chosen.

Of critical importance is the manner by which the two models differ in how the adjacent neighborhood of each location is defined. The first approach (the 'neighbor' model) is based on stochastic local interactions that occur between each location and a random neighbor chosen from any of the locations adjacent to the cell under consideration. Therefore, in this model the spatially interactive neighborhood of each location i is given by the eight adjacent locations that share either an edge or a corner with location i . The second approach (the 'network' model) is also based on local interactions but is constrained such that interactions only occur between each location and its direct downstream neighbor. Therefore in the network model, the neighbor n_j is always given by the adjacent location that is the downstream neighbor of location i . In both models the procedure of probabilistic replacement is repeated until the initially random mosaic of vegetation evolves to a steady state condition in which no further replacements occur ($\sim 10^7$ steps).

The ability of each modeling approach to appropriately characterize the

observed pattern of vegetation distribution within the Rio Salado basin is confirmed through a comparison of the steady-state modified dynamic water stress described above, and the steady-state patterns of tree distribution. The results of the cellular automata modeling reveal that the steady state configuration of the neighbor model (Figure 3c, see page 213) is identical to that of the ideal basin, with vegetation distributed in homogenous swaths based on the underlying variation in climate and soils across the Rio Salado basin. In contrast, the steady state configuration of the network model (Figure 3d, see page 213) is markedly different in character, preserving elements of both the ideal condition, as well as the type of spatial variation exhibited in the actual vegetation pattern (Figure 3a, see page 213).

Figure 4a portrays the basin patterns of water stress resulting from each of these two approaches to dynamic landscape pattern generation, as well as the actual pattern observed within the Rio Salado basin. The results of the three landscape configurations (random, actual and ideal) demonstrate that the current vegetation pattern is configured such that it is well constrained by these two extremes of vegetation organization, so that the basin tends to experience an intermediate level of water stress that is neither random nor ideal (Figure 4a, see page 214). However, the stress profile of the neighbour model (Figure 4b, see page 214) is identical to that of the ideal vegetation (Figure 4a, see page 214), which is consistently lower than that of the actual basin. In contrast, the agreement between the stress profile for the network model and that for the actual basin is much better (Figure 4c, see page 214).

Taken as a whole, these results support the hypothesis that in water controlled ecosystems the drainage network acts as a template for the spatial distribution of vegetation which self-organizes through local stress optimization within the network flow paths of the basin. The feasibly optimal vegetation patterns attained through these simulations correspond to stress profiles around the network that lie between those corresponding to the random and the ideal vegetation distributions.

The above analyses suggest the existence of a balance between the large-scale determinants of vegetation pattern reflecting optimality in the response to water stress and the random small-scale patterns that arise from local factors and ecological legacies such as those caused by dispersal, disturbance, and founder effects. In the Rio Salado basin, we observe an organization that yields an actual pattern of vegetation distribution found to lie within the envelope described by the ideal vegetation pattern that corresponds to the minimization of water stress within the basin, and a random one that preserves the overall percentage of the different types of

vegetation. The dynamic origination of these patterns depends on the structure of the river network itself, which serves as a constraint on the suite of possible vegetation patterns through its effect on the dispersal of vegetation along hillslopes and between subbasins. Having explored the landscape-scale potential for ecohydrological optimization in water-limited ecosystems, we now turn to the role of individual tree canopies on surface hydrological dynamics and their impact on patterns of vegetation structure.

4. ECOHYDROLOGICAL OPTIMIZATION OF LANDSCAPES INFERRED FROM INDIVIDUAL-BASED TREE DISTRIBUTIONS

The structure of terrestrial vegetation communities is strongly governed by the spatio-temporal distribution of growth-limiting resources (Tilman, 1988). However, plants are not passive actors in this regard, and the biotic pattern of vegetation serves to redistribute key abiotic resources such as energy, water, and nutrients in important ways that are critical to the dynamics of the community through space and time. Therefore, any theory regarding the structural configuration of plant communities must explicitly consider the consequences of spatial vegetation pattern on the dynamics of resource availability.

Beginning with the analysis of spatial dynamics in tropical forests (Denslow, 1987), and continuing through the conceptualization of temperate (Runkle and Yetter, 1987) and boreal forest (Bonan and Shugart, 1989) community dynamics, it has become apparent that the nature of plant structural pattern and the dynamics of resource availability are highly interdependent (Tilman and Kareiva, 1997). Although the forest community structure is often thought to be determined by prevailing resource conditions (i.e. climate or soil age), it is now recognized that the forest structure itself serves to modify resource availability. Perhaps best known is the paradigm of gap dynamics – by which species regeneration and subsequent patterns of canopy emergence occur within the localized patches of higher light availability formed by the death of a large canopy tree (Shugart, 1984).

Recently, Caylor *et al.* (2006) proposed a simple model of soil moisture dynamics suitable for application to heterogeneous vegetation landscapes, such as those found in savannas or open woodlands. This approach was intended to provide a framework that can generate hypotheses related to the causes and effects of horizontal variation in soil moisture arising from the patchy vegetation structure of individual tree canopies that is characteristic

of many semi-arid ecosystems. Under the assumption that trees are distributed randomly according to a 2-d Poisson process and have radii drawn from an exponential distribution with mean radius μ_r , the distribution of canopies occurring at any location in the landscape (n_C) follows a Poisson distribution. The focus of this presentation is on the interactions between the number of co-occurring tree canopies (n_C), root systems (n_R), and their combined effect on the overall dynamics of soil moisture. Therefore the quantity $a_i = \mu_R / \mu_r$ is specified as the ratio between the radius of a tree's root system (μ_R) and its associated canopy (μ_r). In this analysis, the value a_i of is assumed to be a fixed property of the vegetation in each landscape. Under the assumption of random tree spacing, tree centers are modeled as a 2-dimensional Poisson process of rate λ_t , where λ_t represents the mean number of centers per unit area. The areal extent of each tree is represented as a circle of random radius, r , drawn from an exponential distribution with mean μ_r . Thus the number, n_C , of canopies occurring at a randomly chosen point has a Poisson distribution (Cox and Miller, 1965) of mean $\langle n_C \rangle = \lambda_t (2\pi\mu_r^2)$, and the expected number of root overlaps is simply $\langle n_R \rangle = 2\pi(\mu_r a_i)^2 \lambda_t$.

The probability of finding a location in the landscape with n_R overlapping root systems and n_C overlapping canopies is the joint distribution n_R of and n_C , notated as $P(n_R \cap n_C)$. Under the condition that the specified ratio of root to canopy areas is set to be one (i.e. $a_i = 1$) so that all root systems are exactly the same size as all canopy areas, it is apparent that $P(n_R \cap n_C) = P(n_R) = P(n_C)$, since each root system is overlain by a single canopy area with probability 1. However, when the root systems are always larger than canopy areas (i.e. $a_i \geq 1$), the joint probability distribution of n_R and n_C is given by $P(n_C | n_R) P(n_R)$, where $P(n_C | n_R)$ is the conditional probability of n_C on n_R . Following the approach presented in Caylor *et al.* (2006), we define the quantity $\tau = 1/a_i^2$, and find that the general form of the conditional probability $P(n_C | n_R)$ is a binomial distribution with mean $n_R \tau$ and variance $n_R \tau (1 - \tau)$.

The distribution $P(n_C \cap n_R)$, for $a_i \geq 1$ is used to connect the distribution of canopies and root systems in the landscape to the soil moisture dynamics which occur therein. In order to assess the ecohydrological organization of individual-based vegetation patterns, we must first determine the distribution of soil moisture, rates of evaporation, plant water uptake, and plant water stress within a structurally heterogeneous landscape of tree canopies and their accompanying root systems. Therefore, we formulate representations of evaporation and plant water uptake governed by n_C and n_R . In particular, we recognize that the parameter n_R determines the local rate of soil

water uptake, while n_C controls the evaporative loss of soil moisture and regulates the partitioning of evapotranspiration into soil evaporation and plant water uptake. The vertical root profile is here assumed to be uniform and individual plant root uptake is evenly partitioned throughout the thickness of a single soil layer, Z_r . Our data on tree active rooting depth is taken from recent field observations of Kalahari root distributions (Hippondoka *et al.*, 2003) which find similar rooting depths across a series of sites in Botswana. Therefore, although the modeling approach could accommodate differences in rooting depth across the transect, we have not included variation in rooting depth between sites. This is in contrast to the regional approach described earlier in this paper that examined the efficiency of vertical niche partitioning as a measure of plant water use.

It is assumed that canopies reduce energy available for evaporation due to shading effects according to an exponential distribution (e.g. Beer's Law), such that $\phi_E(n_C) = e^{-kn_C}$, where ϕ_E is the fraction of incoming energy available for bare soil evaporation under n_C canopies and k is an extinction coefficient of evaporative demand taken to be equal to 0.35 (Brutsaert, 1982). Because root water uptake depends on the amount of energy incident on each root system's corresponding canopy, the plant water extraction rate from the soil is constrained by the total energy absorbed by individual plant canopies. The amount of fractional energy absorption per canopy (φ) for n_C co-occurring canopies is estimated as $\varphi = [1 - \phi_E(n_C)] / (n_C)$. Given a statistical description of the landscape, the exact value of φ for the canopy associated with a particular root system at a random location within the landscape is unknown in this modeling framework. In the absence of specific values of φ for each location in the landscape, we can instead determine the expected amount of energy absorbed per canopy, $\bar{\varphi}$, which we use to constrain water uptake per root system. Finally, we approximate the fraction of potential water uptake that takes place at a location containing n_R root systems (connected to n_R separate canopies) according to $\phi_T(n_R) = \bar{\varphi} \cdot n_R$.

The values of $\phi_E(n_C)$ and $\phi_T(n_R)$ determine the relative amounts of evaporation and plant water uptake at a location with n_C canopies and n_R root systems. At any given location, the sum of evaporation and plant water uptake may exceed the potential evapotranspiration rate (PET mm/day). This is particularly true in open areas that contain many root systems under conditions of high water availability. However, the potential evapotranspiration rate does provide an upper bound on the landscape average evapotranspiration. In addition, the rate of evaporation and plant water uptake both depend on the available soil moisture at any given time. To accommodate

the role of soil moisture limitation on evaporation, we assume that evaporation linearly increases from zero at the soil hygroscopic point, s_h , to a maximum evaporation rate, $\phi_E(n_C) \times PET$, at field capacity, s_{fc} . Similarly, we assume that water uptake from roots (i.e. transpiration) exhibits a linear response to soil moisture availability, increasing from zero at the plant wilting point, s_w , to the maximum, $\phi_T(n_R) \times PET$, at the point of incipient stomatal closure, s^* . At soil moisture values above s^* , water uptake proceeds at the maximum rate, just as evaporation proceeds at the maximum rate above field capacity. Finally, above field capacity, we consider leakage loss from the lower boundary of the soil layer.

At each location in a landscape containing n_C canopies and n_R roots, we consider the water stress distribution according to the frequency and magnitude of excursions of the relative soil moisture below the critical value of s^* that corresponds to the point at which plants begin to close their stomata. Porporato *et al.* (2001) review the physiological impacts of reduced water variability on plant performance and the onset of plant water stress. In order to account for the effects of increasing soil moisture deficit on plant physiological performance, we adopt the formulation of water stress (denoted as ξ) first proposed by Rodríguez-Iturbe *et al.* (1999). Any measure of 'optimal' conditions for plant water use must appropriately balance maximization of resource use with minimization of stress occurrence. For example, as the average root ratio (a_t) increases, an individual plant may be able to increase its plant water uptake rate. However, the increased number of overlapping roots associated with an increase in plant root ratio leads to higher landscape average uptake rates and more rapid onset of stress conditions whenever water becomes limiting. To relate these varying stress and water use patterns to the soil and vegetation parameters, we define an average stress-weighted plant water uptake, $\langle \zeta \rangle$, which is simply the product of the landscape-average plant water uptake rate, $\langle T \rangle$, and the complement of the average plant water stress, $1 - \langle \xi \rangle$, so that $\langle \zeta \rangle = \langle T \rangle [1 - \langle \xi \rangle]$.

The local measure of water stress for a location with n_C canopies and n_R root systems is combined with the joint probability of n_C and n_R to calculate the landscape average value of stress-weighted plant water uptake, $\langle \zeta \rangle$, across the Kalahari rainfall gradient. In particular, we investigate the dependence of $\langle \zeta \rangle$ on the landscape-scale vegetation structural parameters a_t and λ_t . Figure 5 shows the relation between average stress-weighted plant water uptake and the root-to-canopy ratio, a_t at four sites across the Kalahari Transect. As a_t increases, both water uptake and water stress increase, due to the enhanced ability of plants to exploit the soil water resources. At a

critical value of a_t for each landscape, the increase in water stress associated with larger root areas offsets the increase in plant water uptake and the value of $\langle \zeta \rangle$ begins to decrease. This fact explains the existence of an optimal value of a_t in Figure 5 where $\langle \zeta \rangle$ is maximum. The optimal root-to-canopy ratio, a_t , decreases with increasing values of mean annual precipitation, suggesting that sparse semi-arid trees benefit from lateral root growth more than the denser woody vegetation growing in sub-humid environments.

Figure 6 shows the dependence of the landscape averaged value of

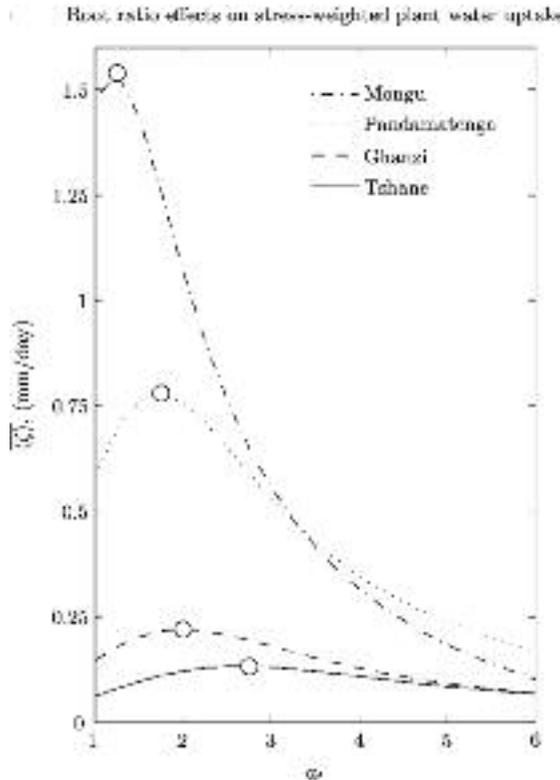


Figure 5. Effect of changing root ratio, a_t , on model predictions of the landscape averaged distribution of stress-weighted plant water uptake, $\langle \zeta \rangle$ (mm/day), within four Kalahari landscapes. The landscape averaged stress-weighted plant water uptake is determined according the product of landscape average daily plant water uptake, $\langle T \rangle$, and the complement of the landscape average daily water stress, $(1 - \langle \zeta \rangle)$. In each of the four landscapes, the maximum landscape averaged stress-weighted plant water uptake (open circle) occurs for increasingly lower values of a_t , as rainfall rates increase, suggesting adaptive changes in the optimal size of lateral root extension across the rainfall gradient. Figure reproduced with permission from Caylor *et al.* (2006).

stress-weighted plant water uptake, $\overline{\zeta}$ mm/day, on tree density, λ_t (ind/m²). Plant water uptake increases with the tree density, while water stress initially decreases with λ_t (i.e. for low values of λ_t), due to the effect of shading on the soil water balance. As a result, an optimal value of tree density exists, which is associated with maximum stress-weighted plant water uptake. This optimal value of λ_t is found to be close to the tree densities observed in the field, suggesting that λ_t changes along the rainfall gradient to optimize the use of the water resources.

5. CONCLUSION

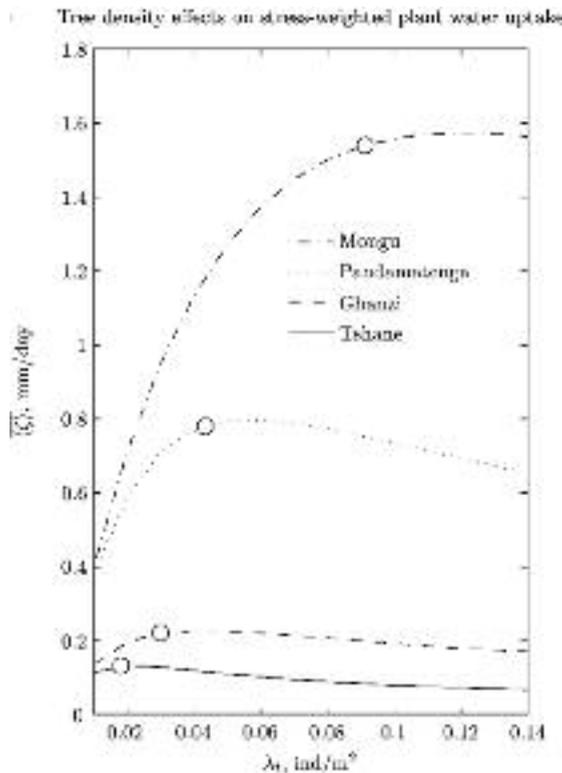


Figure 6. Effect of changing tree density, λ_t , on predictions of the landscape averaged distribution of stress-weighted plant water uptake, $\overline{\zeta}$, within four Kalahari landscapes. All simulations are conducted using the estimated optimal values of root ratio, a_t , determined from Figure 5. Open circles represent the actual density of trees from previous field observations (Caylor *et al.*, 2003) and unpublished data on Ghanzi vegetation. In each landscape, the observed density of trees corresponds to a landscape averaged stress-weighted plant water uptake that is at or just below maximum values across a wide range of possible tree densities. Figure reproduced with permission from Caylor *et al.* (2006).

This chapter has briefly reviewed three efforts to examine the ecohydrological organization of vegetation patterns in water-limited landscapes. In each case, we have tackled a different scale of interest, from regional to individual, through a suite of numerical and analytical modeling approaches. Although the insights gained from each example are derived from specific modeling approaches that each contain their own unique set of assumptions and limitation, they are unified by their use of the water balance and resulting measures of plant water deficit/use as a diagnostic tool for assessing optimality of plant structural pattern. Clearly, such modeling approaches will likely continue to generate hypotheses at a much greater rate than they are able to confirm them. However, it is our hope that the continued development of generalized models capable of assessing a diversity of interactions between plants, soils, and climates will lead to the emergence of more generalized hypotheses regarding the manner by which ecological and hydrological patterns co-organize in landscapes.

6. ACKNOWLEDGEMENTS

K.K.C. and T.M.S. acknowledge the support of NASA's Interdisciplinary Science Program (NASA-NNG-04-GM71G). I.R.-I. acknowledges the support of NSF through grants in Biocomplexity (DEB-0083566) and the National Center for Earth-surface Dynamics (EAR-0120914).

REFERENCES

- Archer, S. (1995), Tree-grass dynamics in a prosopis-thornscrub savanna parkland: Reconstructing the past and predicting the future, *Ecoscience*, 2(1), 83-99.
- Archer, S., Scifres, C., Bassham, C., and Maggio, R., (1988), Autogenic succession in a subtropical savanna: Conversion of grassland to thorn woodland, *Ecological Monographs*, 58(2), 111-127.
- Bonan, G.B., and Shugart, H.H., (1989), Environmental factors and ecological processes in boreal forests, *Annual review of ecology and systematics*, 20, 1-28.
- Brutsaert, W., (1982), *Evaporation into the atmosphere*, D. Reidel Publishing, Boston.
- Caylor, K., Shugart, H., and Smith, T., (2003), Tree spacing along the kala-

- hari transect, *Journal of Arid Environments*, 54(2), 281-296.
- Caylor, K., Dowty, P., Shugart, H., and Ringrose, S., (2004a), Relationship between small-scale structural variability and simulated vegetation productivity across a regional moisture gradient in southern Africa, *Global Change Biology*.
- Caylor, K., D'Odorico, P., and Rodríguez-Iturbe, I., (2006), On the ecohydrology of structurally heterogeneous semi-arid landscapes, *Water Resources Research*, 42(7), 10.1029/2005WR004683.
- Caylor, K.K., Scanlon, T.M., and Rodríguez-Iturbe, I., (2004b), Feasible optimality of vegetation patterns in river basins, *Geophysical Research Letters*, 31(13), 113502.
- Caylor, K.K., Manfreda, S., and Rodríguez-Iturbe, I., (2005), On the coupled geomorphological and ecohydrological organization of river basins, *Advances In Water Resources*, 28(1), 69-86.
- Coughenour, M.B., and Ellis, J.E., (1993), Landscape and climatic control on the woody vegetation in a dry tropical ecosystem: Turkana district, Kenya, *Journal of Biogeography*, 20(4), 383-398.
- Cox, D., and Miller, H., (1965), *A theory of stochastic processes*, Methuen, London.
- Daly, C., Bachelet, D., Lenihan, J.M., Neilson, R.P., Parton, W., and Ojima, D., (2000), Dynamic simulation of tree-grass interactions for global change studies, *Ecological Applications*, 10(2), 449-469.
- Denslow, J.S. (1987), Tropical rainforest gaps and tree species diversity, *Annual review of ecology and systematics*, 18, 431-451.
- Eagleson, P. (1978), Climate, soil and vegetation. 1. A simplified model of soil moisture movement in the liquid phase, *Water Resources Research*, 14(5), 722-730.
- Eagleson, P.S., and Segarra, R.I., (1985), Water-limited equilibrium of savanna vegetation systems, *Water Resources Research*, 21(10), 1483-1493.
- Goward, S.N., and Prince, S.D., (1995), Transient effects of climate on vegetation dynamics: satellite observations, *Journal of Biogeography*, 22(2-3), 549-564.
- Guenther, A., Otter, L., Zimmerman, P., Greenberg, J., Scholes, R., and Scholes, M., (1996), Biogenic hydrocarbon emissions from southern African savannas, *Journal of Geophysical Research-Atmospheres*, 101(D20), 25, 859-25, 865.
- Hippondoka, M., Aranibar, J., Chirara, C., Lihava, M., and Macko, S.,

- (2003), Vertical distribution of grass and tree roots in arid ecosystems of southern Africa: niche differentiation or competition?, *Journal of Arid Environments*, 54(2), 319-325.
- Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T., and Jackson, R.B., (2005), Ecohydrological implications of woody plant encroachment, *Ecology*, 86(2), 308-319.
- Jeltsch, F., Moloney, K., and Milton, S.J., (1999), Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari, *Oikos*, 85(3), 451-466.
- Jeltsch, F., Weber, G.E., and Grimm, V., (2000), Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence, *Plant Ecology*, 150(1-2), 161-171.
- Kim, Y., and Eltahir, E., (2004), Role of topography in facilitating coexistence of trees and grasses within savannas, *Water Resources Research*, 40(W07505), 10.1029/2003WR002578.
- Koch, G.W., Vitousek, P.M., Steffen, W.L., and Walker, B.H., (1995), Terrestrial transects for global change research, *Vegetatio*, 121, 53-65.
- Laio, F., Porporato, A., Fernandez-Illescas, C.P., and Rodríguez-Iturbe, I., (2001), Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress – iv. Discussion of real cases, *Advances in Water Resources*, 24(7), 745-762.
- Levin, S., (1999), *Fragile Dominion: Complexity and the commons*, Perseus Books Group, Reading, MA.
- Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., and Imeson, A.C., (2005), Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes, *Ecology*, 86(2), 288-297.
- Marani, M., Rinaldo, A., Rigon, R., and Rodríguez-Iturbe, I., (1994), Geomorphological width functions and the random cascade, *Geophysical Research Letters*, 21(19), 2123-2126.
- Marani, M., Banavar, J.R., Caldarelli, G., and Rinaldo, A., (1998), Stationary self-organized fractal structures in an open dissipative electrical system, *Journal of Physics – A, General Math*, 31(1018-1024).
- Porporato, A., Laio, F., Ridolfi, L., and Rodríguez-Iturbe, I., (2001), Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress – iii. Vegetation water stress, *Advances in Water Resources*, 24(7), 725-744.
- Privette, J.L., Tian, Y., Roberts, G., Scholes, R.J., Wang, Y., Caylor, K.K., Frost, P., and Mukelabai, M., (2004), Vegetation structure characteris-

- tics and relationships of Kalahari woodlands and savannas, *Global Change Biology*, 10(3), 281-291.
- Ridolfi, L., D'Odorico, P., Porporato, A., and Rodriguez-Iturbe, I., (2003), Stochastic soil moisture dynamics along a hillslope, *Journal of Hydrology*, 272, 264-275.
- Rietkerk, M., Boerlijt, M., van Langvelde, F., HilleRisLambers, R., van de Koppel, J., Kummur, L., Prins, H., and de Roos, A., (2002), Self-organization of vegetation in arid ecosystems, *American Naturalist*, 160, 524-530.
- Rigon, R., Rodríguez-Iturbe, I., and Rinaldo, A., (1998), Feasible optimality implies hack's law, *Water Resources Research*, 34(11), 3181-3189.
- Rodríguez-Iturbe, I., and Rinaldo, A., (1997), *Fractal river basins: Chance and self-organization*, Cambridge University Press, New York.
- Rodríguez-Iturbe, I., D'Odorico, P., Porporato, A., and Ridolfi, L., (1999), On the spatial and temporal links between vegetation, climate, and soil moisture, *Water Resources Research*, 35(12), 3709-3722.
- Rodríguez-Iturbe, I., Porporato, A., Laio, F., and Ridolfi, L., (2001), Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress – i. Scope and general outline, *Advances in Water Resources*, 24(7), 695-705.
- Runkle, J.R., and Yetter, T.C., (1987), Treefalls revisited: gap dynamics in the southern Appalachians, *Ecology*, 68(2), 417-424.
- Sankaran, M., *et al.* (2005), Determinants of woody cover in African savannas, *Nature*, 438(7069), 846-849.
- Scanlon, T.M., and Albertson, J.D., (2003), Inferred controls on tree/grass composition in a savanna ecosystem: Combining 16-year normalized difference vegetation index data with a dynamic soil moisture model, *Water Resources Research*, 39(8), 1224.
- Scanlon, T.M., Albertson, J.D., Caylor, K.K., and Williams, C., (2002), Determining land surface fractional cover from NDVI and rainfall time series for a savanna ecosystem, *Remote Sensing of Environment*, 82(2-3), 376-388.
- Scanlon, T.M., Caylor, K.K., Manfreda, S., Levin, S.A., and Rodríguez-Iturbe, I., (2005), Dynamic response of grass cover to rainfall variability: implications for the function and persistence of savanna ecosystems, *Advances In Water Resources*, 28(3), 291-302.
- Scholes, R., Dowty, P., Caylor, K., Parsons, D., Frost, P., and Shugart, H., (2002), Trends in savanna structure and composition on an aridity gradient in the Kalahari, *Journal of Vegetation Science*, 13(3), 419-428.
- Seyfried, M.S., Schwinning, S., Walvoord, M.A., Pockman, W.T., Newman, B.D., Jackson, R.B., and Phillips, E.M., (2005), Ecohydrological control

- of deep drainage in arid and semiarid regions, *Ecology*, 86(2), 277-287.
- Shugart, H. (1984), *A Theory of Forest Dynamics*, Springer-Verlag, New York.
- Smit, G., and Rethman, N., (2000), The influence of tree thinning on the soil water in a semi-arid savanna of southern Africa, *Journal of Arid Environment*, 44, 41-59.
- Sole, R., Alonso, D., and McKane, A., (2002), Self-organized instability in complex ecosystems, *Philosophical Transactions of the Royal Society of London B*, 357, 667-681.
- Swift, M.R., Maritan, A., and Banavar, J.R., (1997), Scaling properties of sub-optimal interfaces, *Physical Review Letters*, 77, 5288-5292.
- Thomas, D.S., and Shaw, P.A., (1991), *The Kalahari Environment*, Cambridge University Press, Cambridge.
- Tilman, D. (1988), *Plant strategies and the dynamics and structure of plant communities*, Monographs in population biology; 26, Princeton University Press, Princeton, N.J.
- Tilman, D., and Kareiva, P.M., (1997), *Spatial ecology: the role of space in population dynamics and interspecific interactions*, Monographs in population biology; 30, Princeton University Press, Princeton, N.J.
- Turcotte, D. (1990), Implications of chaos, scale-invariance, and fractal statistics in geology, *Global Planetary Change*, 89, 301-308.
- Turcotte, D., and Rundle, J., (2002), Self-organized complexity in the physical, biological, and social sciences, *Proceedings of the National Academy of Sciences of the United States of America*, 99, 2463-2465.
- Walvoord, M., Phillips, F., Stonestrom, D., Evans, R., Hartsough, P., Newman, B., and Striegl, R., (2003), A reservoir of nitrate beneath desert soils, *Science*, 302(5647), 1021-1024, 10.1126/science.1086435.

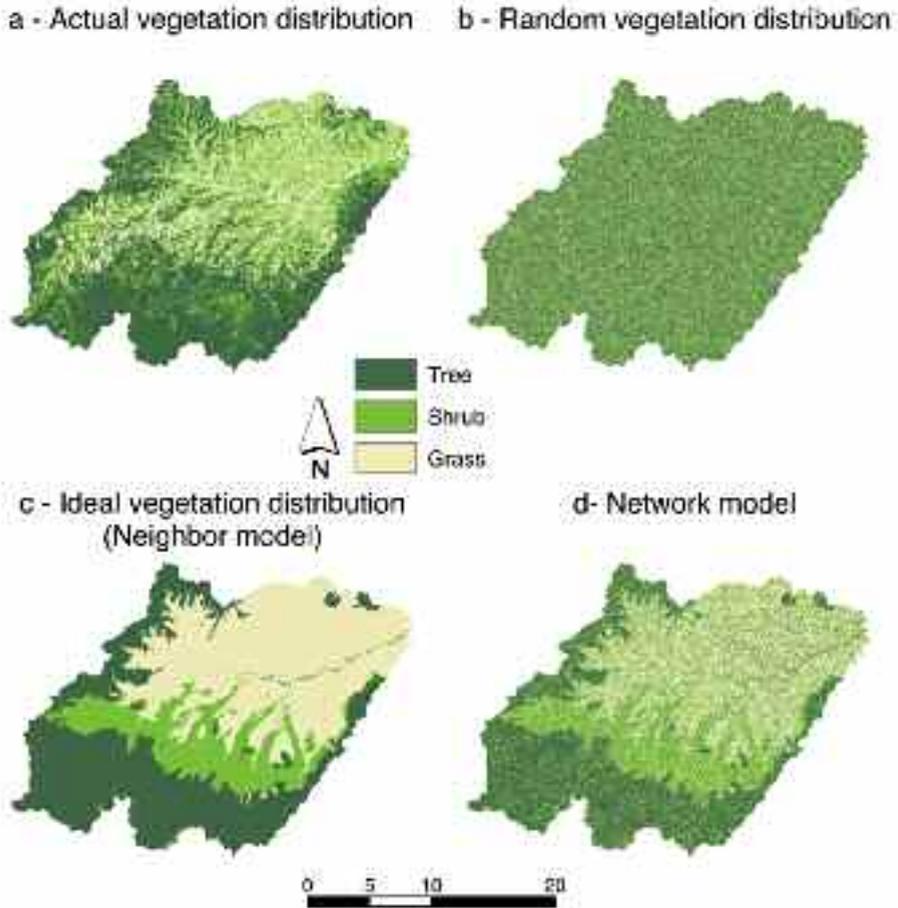


Figure 3. Spatial distribution of land cover within the Rio Salado basin. (a) Actual vegetation distribution in the upper Rio Salado river basin. (b) A random distribution of vegetation representing equal amounts of each land cover type. (c) The pattern of land cover corresponding to an ideal (optimal) pattern that minimizes water stress at each location. (d) A feasibly optimal pattern of vegetation that arises from local optimization within the network flow paths starting from an initially random condition. Scale bar measures distance in kilometers. Figure reproduced with permission from Caylor *et al.* (2004b).

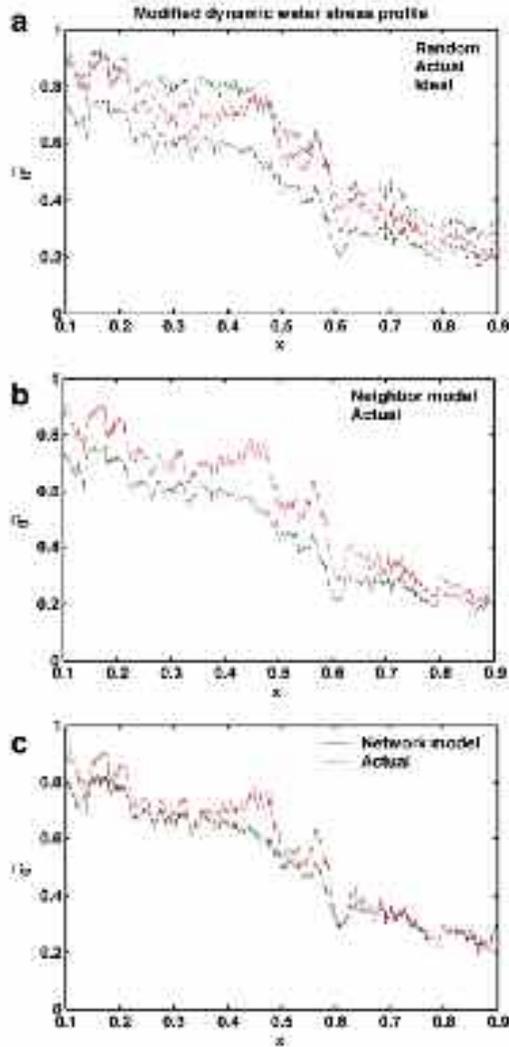


Figure 4. Modified dynamic water stress profiles for the Rio Salado basin, which measures water stress, $\overline{\Theta}$, in the basin according to the normalized flow path distance from the basin outlet, x . (a) Modified dynamic water stress profile for the actual vegetation pattern (red line), a random vegetation pattern (dashed line) and the optimal vegetation pattern (solid line). (b) Modified dynamic water stress profile for the actual vegetation pattern (red line) and the neighbor model at statistical steady state (solid line). (c) Modified dynamic water stress profile for the actual vegetation pattern (red line) and the network model at statistical steady state (solid line). Figure reproduced with permission from Caylor *et al.* (2004b).