Role of topography in facilitating coexistence of trees and grasses within savannas

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[1] The factors and processes that may explain the observed coexistence of trees and grasses in savannas are not well understood. Here we propose a new hypothesis that addresses this issue. We hypothesize that "variations in elevation at relatively short horizontal scales of ~1 km force similar variations in soil moisture and thus create significantly different hydrologic niches within any large area. Under water-limited conditions the relatively wet valleys favor trees, while the relatively dry hills favor grasses. This coexistence of trees and grasses is only possible for a window of climatic conditions that are characteristic of savannas." To test this hypothesis, numerical simulations are performed for the region of West Africa using a model that simulates vegetation dynamics, the Integrated Biosphere Simulator (IBIS), and a distributed hydrologic model, Systeme Hydrologique Europeen (SHE). IBIS is modified to include the groundwater table (GWT) as a lower boundary. The spatial distribution of GWT is simulated by SHE. At 9°N the model simulates trees even when the GWT is assumed to be infinitely deep; at 13°N the model simulates grasses even when the capillary fringe of the GWT reaches the surface. However, for the transitional climate, at 11°N, trees are simulated when the GWT is at ~2.5 m from the surface, but grasses are simulated when the GWT is deeper than 2.5 m. These results suggest that the variability of soil moisture forced by topography can be a determinant factor of vegetation distribution within savannas. Furthermore, they confirm that this role of topography can be significant only in a certain climatic window characteristic of savannas. *INDEX TERMS:* 1851 Hydrology: Plant ecology; 1719 History of Geophysics: Hydrology; 1833 Hydrology: Hydroclimatology; *KEYWORDS:* coexistence, savannas, topography, West Africa

1. Introduction

[2] Savanna ecosystems, a mixture of trees and grasses, constitute one of the world's major biomes and occupy ~20% of the land surface. They are defined as tropical or near-tropical ecosystems with a continuous herbaceous grass layer and a discontinuous layer of trees and/or shrubs [*Skarpe*, 1992]. Savannas often occupy the buffer zone between the equatorial forests and the midlatitude deserts. Their ecology is neither that of grassland nor that of a forest [*Scholes and Walker*, 1993]. The complex interaction of trees and grasses shapes their ecological characteristics, and their coexistence still remains not fully understood.

[3] In the classical description of how dominant vegetation types are selected, one plant type becomes dominant when it outcompetes the others over the same resources (light, water, and nutrients). In savannas, however, two competitors, trees and grasses, often coexist under the same climatic conditions. Here we are interested in defining what conditions allow them to survive together. There are two general theories on savannas, which are described here as equilibrium and disequilibrium theories.

[4] The equilibrium theory suggests that the coexistence of different vegetation types is dynamically stable. Different species compete for water, light, and nutrients, and then an equilibrium is achieved in savannas, as it is elsewhere. The focus is on the water-limited arid and semiarid savannas. *Walter* [1971] hypothesizes that water availability is the determinant factor for semiarid savannas. While grasses only exploit the shallow soil moisture, trees and shrubs can access the soil water of the deep soil as well as that of the shallow soil. Hence the two plant types coexist by exploiting two different reservoirs of water. On the basis of Walter's hypothesis, several models have been developed to describe savannas. *Walker et al.* [1981] developed an analytical model that illustrates this hypothesis and shows a stable equilibrium characterized by a mixture of trees and grasses. Roots of grasses are restricted to shallow soil layers, so they have priority in exploiting soil water from shallow soils. Trees extend their roots to shallow and deep soil layers, but they are outcompeted by grasses in the surface soil. Consequently, grasses utilize the soil water from the surface soil, and trees utilize the water from the deep soil. As a result, trees and grasses coexist in savannas.

[5] *Eagleson and Segarra* [1985] bring a second dimension to this discussion. They emphasize the competition of trees and grasses for light as well as water. They assume that

trees have an advantage in their access to light compared to grasses. Trees only use water from the deep soil that grasses cannot use. However, trees limit the water use of grasses by shading them from the solar radiation. Their two-layer model simulates three equilibrium states, according to specified parameters, which are forests, grasslands, and savannas. They show that savannas are only one ecosystem, stable to perturbations such as fires.

[6] Most of the above discussion focused on competition in the vertical dimension. Recently, *Rodriguez-Iturbe et al.* [1999] developed a new model to address the role of horizontal spatial dynamics in facilitating coexistence of trees and grasses. Their model has been tested for the savanna climate of Nylsvley in South Africa. They argue that the spatial competition, in the horizontal direction, on water must be included in order to explain the coexistence of trees and grasses. The model allows horizontal competition between trees and grasses and between trees themselves or grasses themselves. In the model a grid cell is occupied by a tree or grass. Then, species in neighboring cells can exploit the soil water from the next cell. The water stress corresponding to the canopy densities of trees and grasses is described explicitly while allowing their spatial competition for soil moisture. The results show that a mixture of trees and grasses exists under a minimum water stress, i.e., the optimal condition.

[7] In a different approach to the study of savanna the disequilibrium theory suggests that disturbance mechanisms such as fires and climate fluctuations play a significant role in facilitating the coexistence of trees and grasses. Disturbance mechanisms prevent savannas from developing into a simpler ecosystem such as grassland or forest. Fires, droughts, and grazings are disturbances forced from outside the ecosystem [*Skarpe*, 1992; *Scholes and Walker*, 1993; *Bourliere and Hadley*, 1983]. For example, *Skarpe* [1992, p. 293] argues that "Most savannas, particularly African ones, are believed to owe their existence more to the impact of fire and large herbivores than to climate, and these factors seem largely to determine the boundary between savanna and forest."

[8] *Scholes and Walker* [1993] performed a field experiment at the savannas of Nylsvley in South Africa. From measurements in the broad-leafed savanna they found that the grass roots use subsoil water as efficiently as tree roots and that tree roots dried out the topsoil as much as grass roots alone. Therefore the competition for the available water is not important in shaping savannas. Instead, they argue that savannas are shaped by fires, droughts, herbivores, frost, lightning, and wind.

2. Hypothesis

[9] To describe how trees and grasses coexist in savannas, we propose a different hypothesis. Our hypothesis states that "variations in elevation at relatively short horizontal scales (∼1 km) force similar variations in soil moisture and thus create significantly different hydrologic niches within any large area. Under water-limited conditions the relatively wet valleys favor trees, while the relatively dry hills favor grasses. This coexistence of trees and grasses is only possible for a window of climatic conditions that are characteristic of savannas" (see Figure 1).

[10] The satellite-based observations in Figure 2 shed some light on the proposed hypothesis. For the elevation field in Figure 2a we use a global digital elevation model with a horizontal grid spacing of 30 arc sec (GTOPO30) from U.S. Geological Survey's EROS Data Center (available at http://edcdaac.usgs.gov/gtopo30/gtopo30.asp). Moderate Resolution Imaging Spectroradiometer 500 m Global Vegetation Continuous Fields (VCF) data from 2000 to 2001 (available at http://modis.umiacs.umd.edu/vcf.htm) are used to generate 30 arc sec (∼1 km) VCF data, which are shown in Figures 2b and 2c. The region described by these data falls in the West African savannas. These data show that the fractional coverage of trees is larger along the valley than on the hills. Hence we suggest that our hypothesis can be one possible explanation about savanna existences even though it is not the only plausible explanation for all regions occupied by savanna ecosystem.

[11] The spatial variation of soil water contents is influenced by many factors: the variations of topography, soil property, water table depth, vegetation type, and atmospheric forcings. In this study, however, the topographic effects on the soil moisture distribution are emphasized. Topography primarily influences the soil moisture distribution through the variation of relative elevation, slope, and upslope drainage area. The rain falling on a watershed is redistributed through the runoff-producing mechanisms during and after the rainfall events. The storm runoff takes place in the form of overland flow, interflow, and subsurface flow. In general, water converges into the concave area, near the channels, from the convex areas of the hill slope. The relatively low elevation, hollow slope, and shallow water table make valleys wetter than hills.

[12] Now the ecology of grasses and trees is considered. Plants compete for light above the ground and for water and many mineral nutrients under the ground [*Casper and Jackson*, 1997]. Furthermore, plants in a water-limited ecosystem are often stressed by both the water availability and the nutrient availability [*Porporato et al.*, 2003]. Since the hydrologic cycle is associated with the soil carbon and nutrient cycles through various ways (e.g., plant root uptakes, plant growth and leaching) in the plant ecosystem, the water availability is essential in semiarid and arid regions, where the hydrologic environment may not favor growth of plants. In nature, trees and grasses compete for water, and they utilize it in different ways. Grasses transpire very actively even under water stress; that is, they can grow under relatively low annual rainfall. Grasses just need water during the growing season. On the other hand, woody plants require much more water to grow, and they absorb water even during the dormant period. Different climates favor different types of vegetation. In savannas, however, ecologically different types of vegetation coexist under the same environment.

[13] Here we emphasize that topography creates different hydrologic niches with significant ecological implications. The concave area along the valleys has more water than the convex areas of the hill slopes. These relatively moist soils along the valleys can support trees, even when the less moist soils over the hills can only support grasses but not trees. Hence trees and grasses can coexist in response to the variation of elevation, even under the same climate condition.
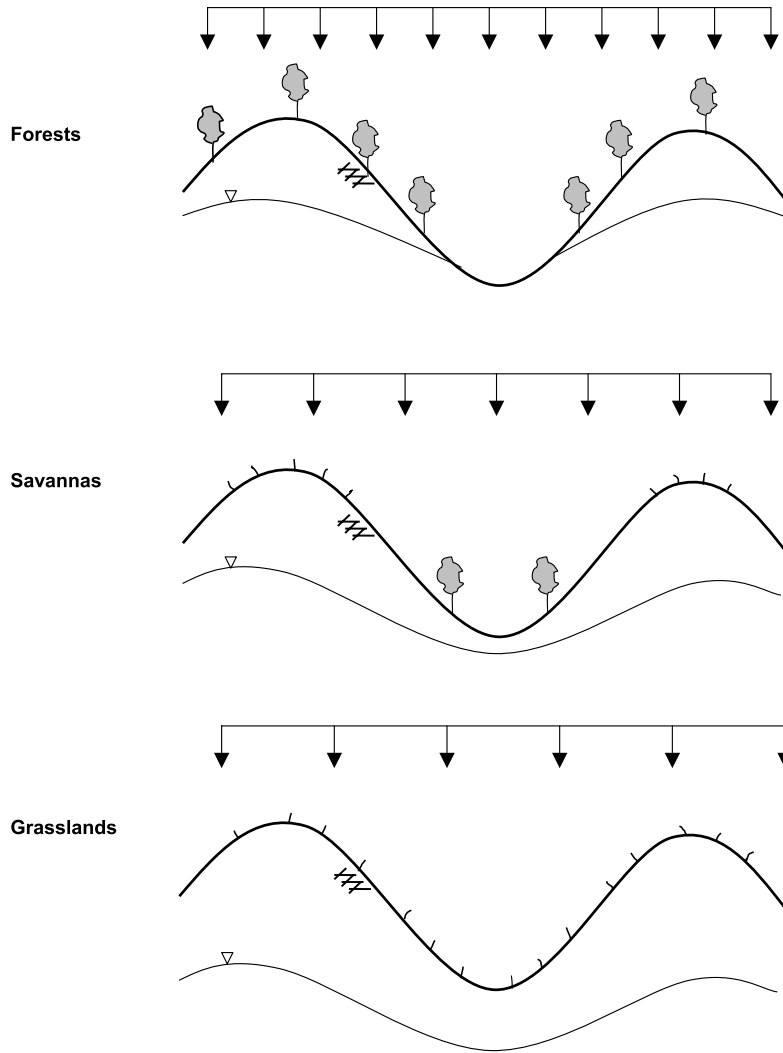
Figure 1. Schematic illustration of new hypothesis, presenting that variations in elevation can facilitate the coexistence only for a window of climate conditions that are characteristic of savannas.

[14] *Jeltsch et al.* [2000] proposed a unifying theory of long-term tree-grass coexistence based on the concept of ecological buffering mechanisms. They focused on the boundaries of savanna and investigated the mechanisms that allow savanna to persist in the critical situations where the system is driven to its boundaries, e.g., pure grasslands or forests. Fire and browsers were suggested by *Jeltsch et al.* [2000] as the main mechanisms preventing savanna from
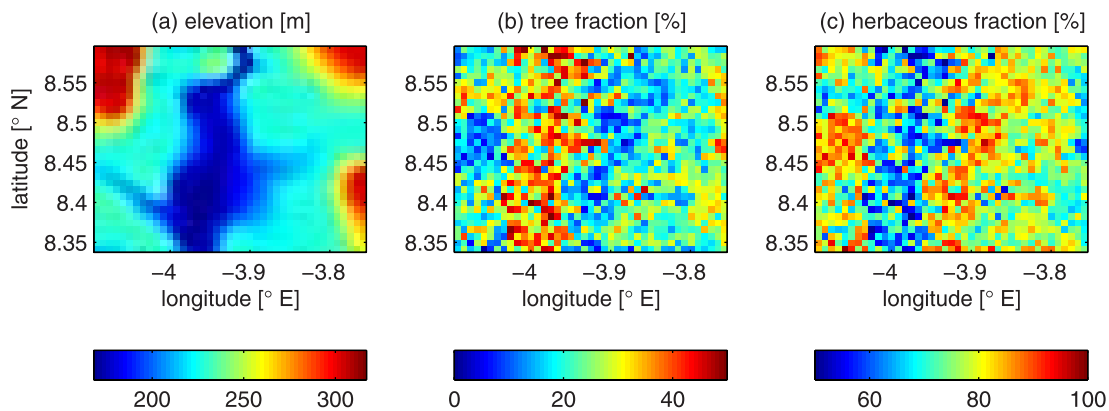

Figure 2. Geographic distribution of (a) topography, (b) tree fractional coverage, and (c) herbaceous fractional coverage in a region (4.0917°−3.7583°W and 8.3417°−8.5917°N) of West African savannas.
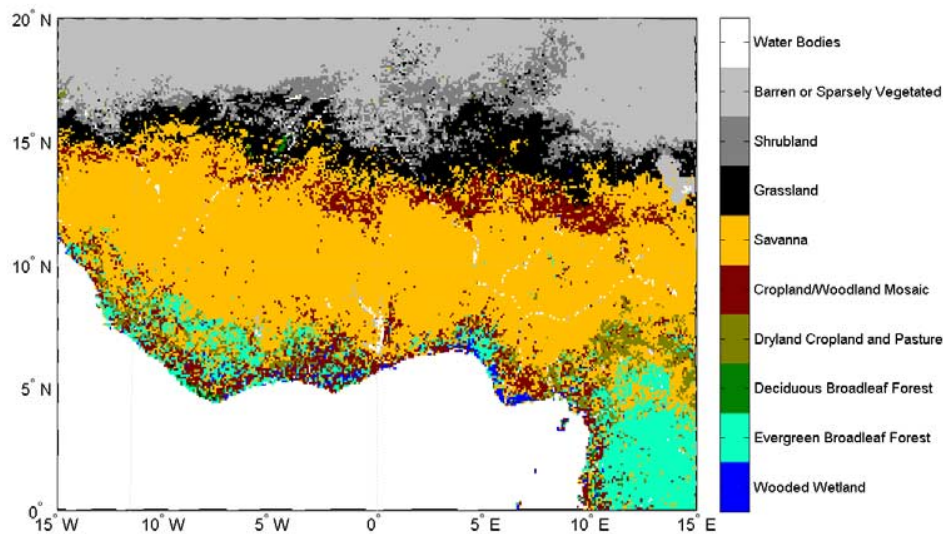
Figure 3. U.S. Geological Survey land cover classification. Savannas occupy extensive area of West Africa.

developing into forests. This process has been illustrated by *Wang and Eltahir* [2000a] using a modeling approach. *Jeltsch et al.* [2000] also discussed the concept of microsites favoring tree establishment and survival as a buffering mechanism that prevents savanna from developing into grasslands. The hypothesis presented in this paper is consistent with this concept of microsites and emphasizes the role of topography in creating these microsites or niches.

3. Study Area

[15] In this paper, we focus on West African savannas. West Africa is defined here as the region between the Sahara desert to the north and the Atlantic coast to the south, between 15°W and 15°E. Savannas occupy wide areas of West Africa, as seen in Figure 3, roughly located between 7° and 12.5°N [*Anderson et al.*, 1976; *Foley et al.*, 1996].

[16] West Africa is located in the tropical climate zone and falls under the influence of a regional monsoon circulation. The annual rainfall exhibits a sharp meridional gradient ranging from over 2000 mm near the coast to <200 mm at the border of Sahara desert. A weak zonal gradient is observed near the western coast but is absent elsewhere. Moreover, the climate of West Africa has a strong seasonality with a wet summer and a dry winter. Most of the rainfall events are limited to the wet season. The duration of rainy season also has a meridional gradient, which ranges from ∼5 months in the coastal region to 1 month at the desert margins. The zonal symmetry and the seasonal variability in West Africa are primarily shaped by the West African monsoon circulation.

[17] Climate is the primary factor that determines the distribution of vegetation. The sharp meridional gradients of the important climate variables such as rainfall and temperature make the distribution of the dominant vegetation type roughly parallel to the latitudinal lines. The coastal region has access to abundant water and solar radiation, which is enough to support trees, making humid forests the dominant vegetation type. The amount of rainfall decreases northward. The area around the desert border is under water

stress. Grasses can survive with relatively less water than trees since grasses transpire efficiently with shallow roots. Consequently, grasses are the dominant vegetation type in the north. In other words, the ecosystem changes from forests at the coastal region to grasslands at the northern edges. Between forests and grasslands, savannas exist as a transitional zone.

4. Models

[18] In this study, we use a biospheric model and a distributed hydrologic model. One experiment is performed only using the biospheric model, and the other is carried out by asynchronous coupling of the biospheric model and distributed hydrologic model. The biospheric model is the Integrated Biosphere Simulator (IBIS) [*Foley et al.*, 1996] which describes biophysical, physiological, and ecological processes. The distributed hydrologic modeling is performed using Systeme Hydrologique Europeen (SHE) [*Abbott et al.*, 1986a, 1988b]. These two models are described in sections 4.1 and 4.2.

4.1. Biospheric Model

[19] IBIS models an extended range of terrestrial processes under given atmospheric conditions. These conditions include air temperature, precipitation, specific humidity, cloudiness, and solar and longwave radiation. The vegetation cover in IBIS is described by a combination of plant functional types (PFTs) in order to represent vegetation dynamics. The plant functional types are defined on the basis of ecological characteristics: physiognomy (trees and grasses), leaf habit (evergreen and deciduous), photosynthetic pathway (carbon 3 and carbon 4), and leaf form (broad leaf and needle leaf). Each of the PFTs has different responses to the given climate. The success of any PFT is reflected in its leaf area index (LAI) and carbon biomass.

[20] IBIS has hierarchical and modular structure with four modules: land surface module, vegetation phenology module, carbon balance module, and vegetation dynamics

module. These modules are independent and operate with different time steps. The land surface model is integrated on a time step between 10 and 60 min, the vegetation phenology model is integrated on a daily timescale, and carbon balance and vegetation dynamics models are integrated on an annual time step.

[21] The land surface module simulates the exchange of energy, water vapor, carbon dioxide, and momentum between the surface, the vegetation canopies, and the atmosphere on a time step of 60 min in this study. It is noted that for the soil bottom boundary, drainage is computed by multiplying an empirical coefficient with the unsaturated hydraulic conductivity. Such representation ignores the role of groundwater table as a lower boundary. This aspect of the scheme will be modified.

[22] The vegetation canopy is divided into two layers, with the woody plant functional types in the upper canopy and herbaceous plant functional types in the lower canopy. The vegetation canopies extend their roots into the soil layers with canopy-specific root density distribution. This two-layer canopy model and canopy-specific root density distribution allows the competition among different plant types for light and water, respectively. More details on IBIS are offered by *Foley et al.* [1996].

[23] IBIS was originally developed to describe processes over large areas. However, since it assumes homogeneous spatial conditions, we apply IBIS in this study to describe biospheric processes at the local scale.

4.2. Distributed Hydrologic Model

[24] SHE models the hydrologic processes at the watershed scale. The spatial distribution of basin parameters, meteorological inputs, and hydrologic responses are represented in a grid cell of vertical layers. The water fluxes are described in a finite difference representation of the physical equations (the partial differential equations describing mass, momentum, and energy conservation) or empirical equations. SHE has a modular structure. These modules describe overland flow, channel flow, evapotranspiration, unsaturated flow, and saturated flow. Each module runs independently; then all are linked in order to exchange water among different components. Furthermore, *Graham and Klide* [2002] provide the detailed description of the governing equations and numerical scheme.

5. Experiment 1

5.1. Design of Experiments

[25] This section presents a preliminary set of experiments designed to test the hypothesis in section 2 using IBIS. However, IBIS has two limitations that need to be addressed.

[26] First, IBIS does not simulate a savanna as an equilibrium land cover over West Africa or elsewhere [*Wang and Eltahir*, 2000a]. The model evolves into the equilibrium with the tropical deciduous forest at 9°N, and the grassland at 11°N, but in nature, savannas are observed at 9° and 11°N (see Figure 3). The disagreement of model results has been attributed to the lack of disturbance mechanism, such as fire, and interannual climate variability [*Foley et al.*, 1996]. To test this argument, *Wang and Eltahir* [2000a] performed simulations assuming a certain frequency of fire and grazing on the savanna region using

IBIS. It is assumed that fires take place every year during the dry season and consume a fraction of 0–10% of the aboveground biomass. The exact fraction is simulated from a uniform distribution. Grazing consumes 50% of grasses every year. Under these assumptions the model simulates savanna-type vegetation near 11°N. This result supports the disequilibrium theory about the savanna dynamics. However, without external disturbance, IBIS simulates a simple equilibrium state, grasslands or forests, over the West African savannas.

[27] Second, the model assumes a flat plain over the domain. Instead of directly presenting the variation of elevation we vary the amount of rainfall as the input. The variation of rainfall inputs is a surrogate for the difference of soil water contents at different areas over a region. A hill area will have less soil water than a valley area since water converges to hollow valleys through runoff. More available water at a valley is represented by more rainfall input for a valley than for a hill area.

[28] Consequently, the experiments are designed to simulate the different vegetation types, grasslands or forests, while varying the amount of rainfall input. In other words, if the alternative equilibrium states (grasslands or forests) are simulated only by adjusting rainfall input amounts, trees and grasses may coexist in the same region. For instance, forests are predicted in 9°N under the normal condition, and then we reduce the amount of rainfall input until grasslands are simulated as equilibrium. Furthermore, we determine the range of rainfall input amounts between "valleys" (where trees are simulated) and "hills" (where grasses are simulated). Its extent should fall into a reasonable range, where the variation of local topography may naturally redistribute water over the region. In addition, hereinafter, the term rainfall factor (RF) is used as the factor (e.g., 0.8, 1.2, and 1.5), multiplying the normal amount of rainfall, which represents the effective rainfall amount reaching the area.

[29] Our experiments are performed in three areas, 9°, 11°, and 13°N. In natural savannas, 9° and 11°N, we expect the transition from grasslands to forests (or from forests to grasslands) while we adjust the rainfall. Also, the natural grassland area, 13°N, is selected for the experiment, expecting that in this case any reasonable modification of rainfall input should not result in the transition to forests.

[30] The climatology of daily air temperature, relative humidity, wind speed, precipitation, and fractional cloud cover at three latitudes (9°, 11°, and 13°N) are used for the simulations. The data are taken from the National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) Reanalysis Project. The data during 1958–1997 are averaged between 15°W and 15°E (see Figure 4). Supplemental rainfall data are taken from the Hydrologic Atmosphere Pilot Experiment (HAPEX)-Sahel project (1991–1994) for the area of 13°N. The simulations at 13°N are performed twice with NCEP/NCAR reanalysis data and with HAPEX-Sahel field data. The daily temperature and specific humidity are interpolated to an hourly resolution assuming a sinusoidal diurnal cycle. The length of a precipitation event in a day is randomly determined between 4 and 24 hours, assuming it follows uniform distribution.

[31] As pointed out before, the IBIS can be coupled with an atmospheric model. In this study, however, the IBIS is
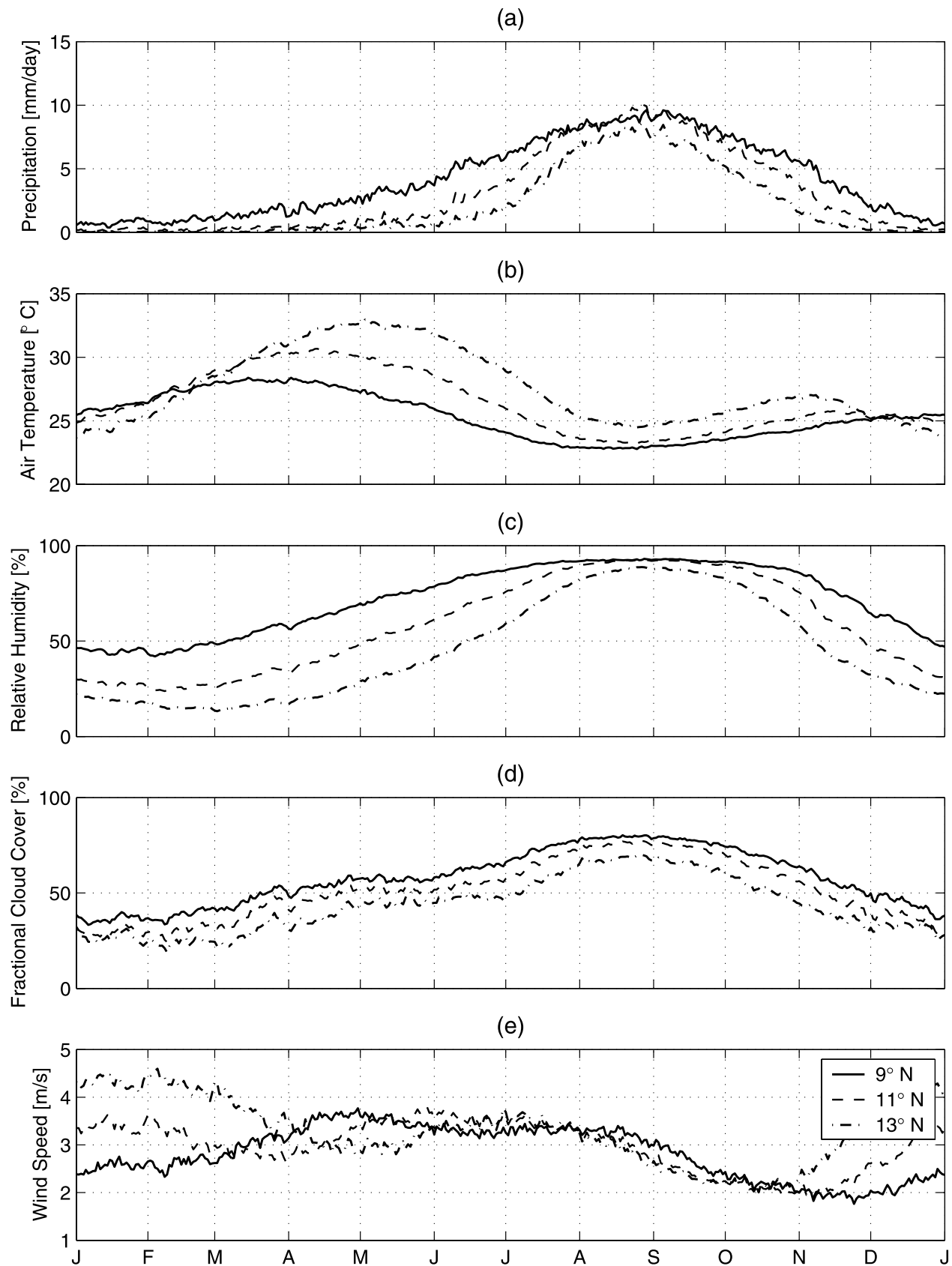
Figure 4. Seasonal cycle of (a) precipitation, (b) air temperature, (c) relative humidity, (d) fractional cloud cover, and (e) wind speed at 9° (solid), 11° (dashed), and 13°N (dash-dotted).
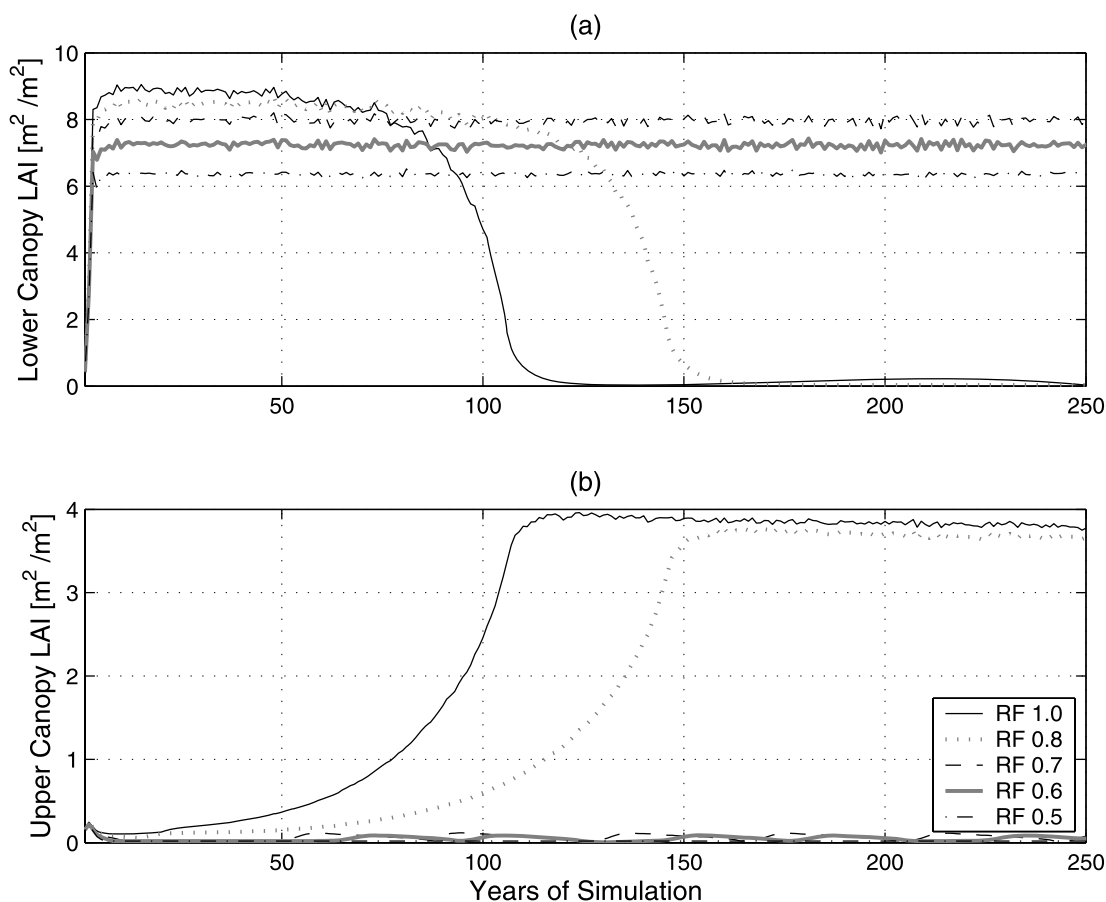
Figure 5. At 9°N, change of the leaf area index (LAI) of (a) lower canopy and (b) upper canopy during the simulation.

used off-line, without two-way interaction between the atmosphere and biosphere. Moreover, simulations in this set of experiments are performed assuming a free gravitational drainage condition at the bottom. This assumption will be relaxed later. As explained in section 4, the original model describes the upper soil layers only down to 4 m. The discharge from the soil bottom is described by a simple coefficient multiplying the unsaturated hydraulic conductivity of the bottom layer. This coefficient ranges from 0 (no flux) to 1 (free gravitational drainage). More discussion about the lack of groundwater aquifers in the model will be presented in section 6.

[32] At the beginning of each simulation, all PFTs have the same minimal LAIs of 0.1. Each type of vegetation has equal opportunity to survive at the start time, and then they compete with each other for water and light under the given atmospheric condition. Simulations run for 250–500 years to give enough time to reach equilibrium state. We determine if the model is close to the equilibrium by monitoring the annual changes of LAI of upper and lower canopies. A stable state of LAIs is a characteristic of the equilibrium state.

5.2. Results

5.2.1. Results at 9°N

[33] The model predicts a dry deciduous forest under the normal rainfall levels at 9°N. To determine the rainfall level

where the transition to grasses takes place, the total annual rainfall is decreased gradually. With 0.7 times the typical rainfall amounts the transition from dry forests to grasslands takes place. Figures 5a and 5b show the change of lower LAI and upper LAI, respectively, during the simulation. Since the model is initialized with the equal, minimal amount of seeds of all PFTs, the lower canopy PFTs flourish in the beginning of simulation. Then, the upper canopies grow high enough and outcompete the grasses in their competition for light. The two-layer canopy model implemented in IBIS prioritizes light resource to the upper canopy, and hence trees dominate grasses under enough available water resource. In the case of RF of 0.7, LAI of lower canopy stays at the constant level around 8, and LAI of upper canopy does not increase but keeps its low level. Grasses outcompete trees in their competition for the limited water input. This shows grasslands are stable as the equilibrium ecosystem with RF of 0.7.

5.2.2. Results at 11°N

[34] With normal rainfall levels the model simulates grassland equilibrium at 11°N. Contrary to the case of 9°N, here we need to increase the annual rainfall in order to test if we can get a transition from grasslands to forests. At RF of 1.9, grassland is simulated as the equilibrium state. However, at RF of 2.0 with annual rainfall of ~2240 mm, a tropical deciduous forest is simulated as the equilibrium. As shown in Figure 6, LAI of the lower canopy stays around 6
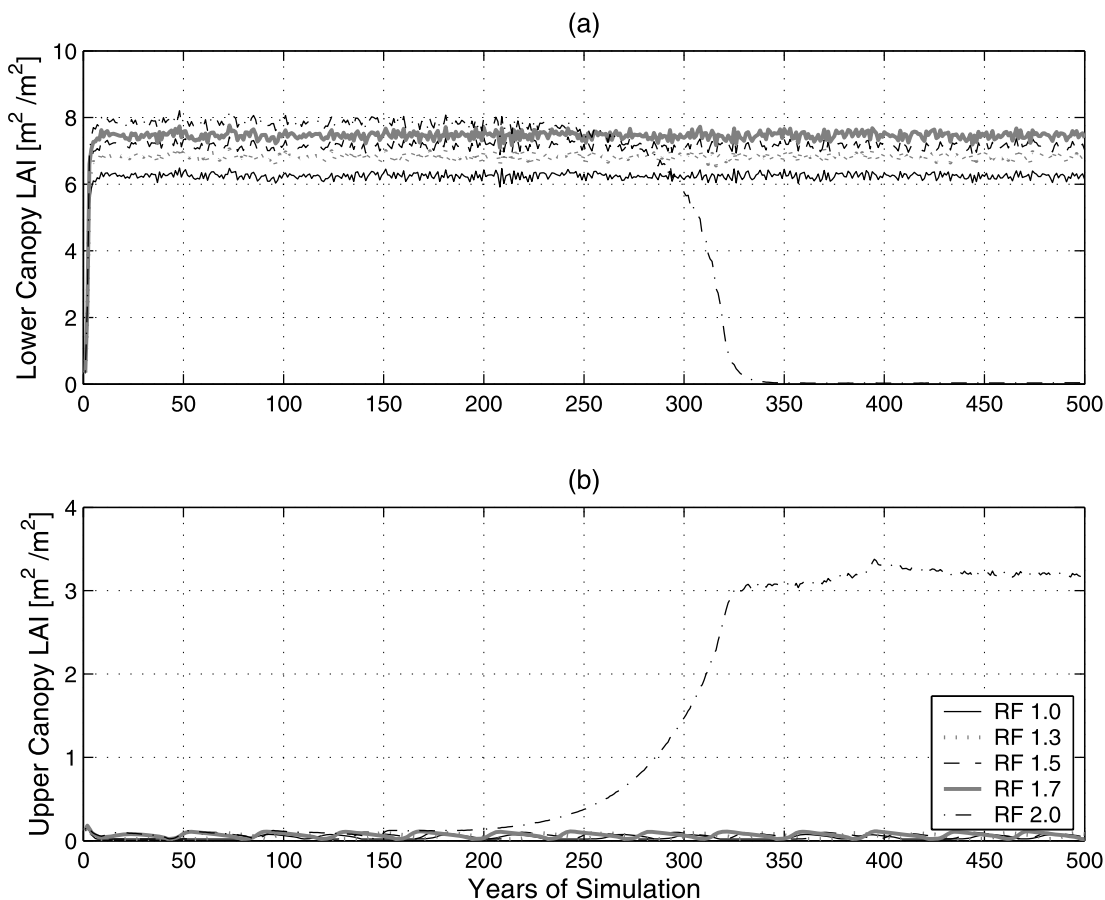
Figure 6. At 11°N, change of the leaf area index (LAI) of (a) lower canopy and (b) upper canopy during the simulation.

under the normal conditions. At RF of 2.0, however, the lower canopy LAI decreases, and the upper canopy LAI starts to increase after around 200 years. To confirm that the model converges to forest equilibrium, the simulation is run for 500 years, which is different from the other simulations (250 years). In summary, in response to the adjustment of rainfall inputs, both forests and grasslands are simulated at 11°N where savannas are naturally observed.

5.2.3. Results at 13°N

[35] For the case of 13°N, two sets of simulations are performed. First, all the meteorological data are taken from NCEP/NCAR Reanalysis Project similar to the above cases of 9° and 11°N. Second, only the rainfall input is replaced by the field measurements of HAPEX-Sahel. As seen in Figure 7, the field measurements of rainfall show the seasonality of rainfall distribution more clearly than the
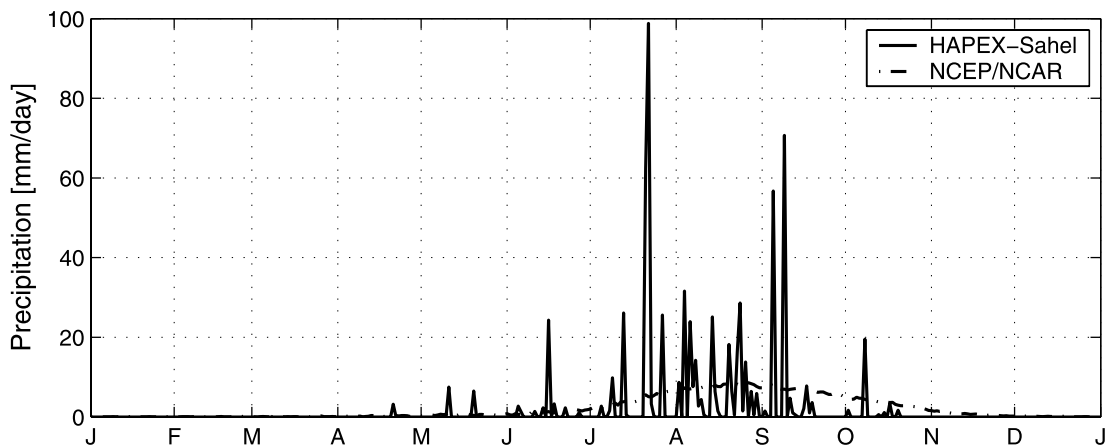

Figure 7. Seasonal cycle of precipitation at 13°N from NCEP/NCAR (dash-dotted) and HAPEX-Sahel (solid).
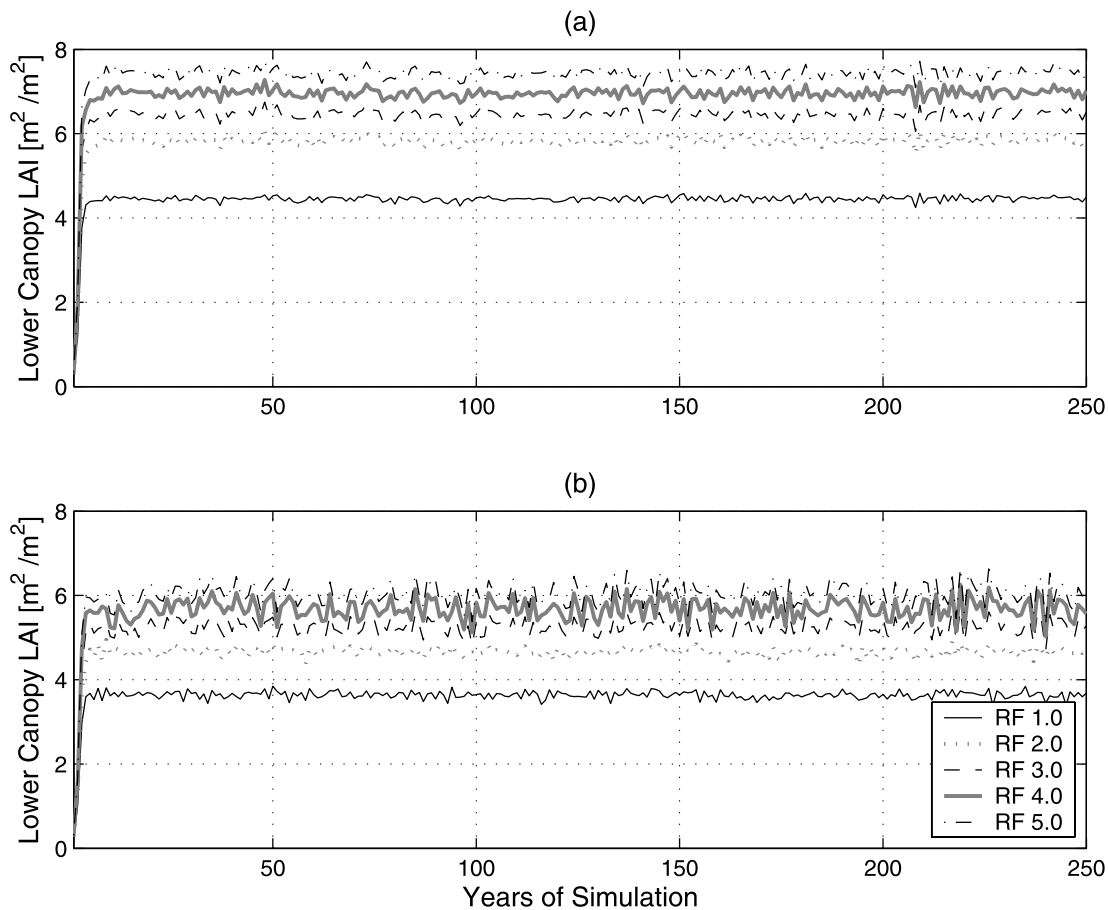
Figure 8. At 13°N, change of the leaf area index (LAI) of lower canopy during the simulation with the precipitation from (a) NCEP/NCAR and (b) HAPEX-Sahel.

reanalysis data. The annual accumulated precipitation is not much different between them, with 0.77 and 0.69 m in NCEP/NCAR and HAPEX-Sahel, respectively. However, the data from HAPEX-Sahel show the intense rainfall during a wet summer. The reanalysis data present less intense and more frequent storms throughout the year.

[36] In the land cover observations the region at 13°N is the northern boundary of savannas and consists of grasslands. With the NCEP/NCAR forcing, the equilibrium vegetation is grassland under the normal condition. Thus the amount of rainfall input needs to be increased to test any possible changes in the simulated equilibrium conditions, similar to 11°N. As seen in Figure 8, the transition from grasslands to forests does not take place for all rainfall increases that have been considered. We get the same results using the HAPEX-Sahel rainfall data. Even using 5 times the normal rainfall, the model still simulates grasslands as the equilibrium ecosystem in both cases.

5.3. Summary

[37] This set of experiments is designed to estimate the amount of rainfall required for trees and grasses to dominate under a certain atmospheric condition. At 9°N, tropical deciduous forests are simulated with the normal rainfall, and grasslands are simulated with a 30% decrease in rainfall. At 11°N, grasslands are simulated with the normal rainfall levels, and deciduous forests are simulated with a 100% increase of the rainfall input. At 13°N the model simulates only grasslands as the equilibrium ecosystem, regardless of the rainfall input.

[38] Topography drives lateral transport of water. Water converges into concave areas through surface or subsurface runoff. In a dry region the surface runoff occurs often because of the infiltration excess mechanism, not the saturation excess. Furthermore, the West African savannas occupy a region where the intense rainfall events are limited to the summer season, and the surface soils may hardly be saturated. In dry hills the rainfall intensity exceeds the infiltration capacity of the dry soils, and the excess water converges into the relatively wet valleys. Similarly, the depth to the water table is significantly shallower over the valleys compared to the hills. Capillary rise of water would tend to moisten the soil profiles at the root zones more significantly over valleys compared to hills. Therefore relatively dry hills and wet valleys are likely to coexist over any savanna region. Both 30% (at 9°N) and 100% (at 11°N) differences in soil moisture between hills and valleys are plausible. Spatial variability of soil moisture conditions can be an important factor in order for trees and grasses to coexist. Over the grassland region at 13°N any reasonable degree of moisture redistribution is not enough to create niches that are favorable for trees. Simple increases or decreases of available water amounts are enough to create the conditions favorable to the different types of plants only

for a specific climatic window that is characteristic of natural savannas (9° and 11°N).

6. Experiment 2

[39] The same hypothesis is tested in another set of experiments, using a modified version of IBIS. The soil model of IBIS is modified to include the groundwater table (GWT) as the lower boundary. This modification facilitates studying the response of IBIS to variations in the depth to the GWT [*Yeh*, 2003]. The variation in GWT over a region can be simulated with SHE. Such variations reflect the spatial variability of elevation that has been suggested to explain the coexistence of trees and grasses within savanna.

6.1. Methodology Using IBIS and SHE

[40] The level of GWT is highly correlated with soil moisture. The variation of soil moisture can dictate different types of vegetation, trees or grasses, given the climate of savannas as illustrated in the previous set of experiments. Consequently, it is postulated that the spatial variability of GWT facilitates coexistence of trees and grasses in a region. A shallow GWT provides more water to the soil and vegetation than a deep one. Using IBIS, however, this cannot be tested in a direct way, since the original model does not represent the GWT.

[41] The land-surface transfer scheme (LSX) model [*Pollard and Thompson*, 1995; *Thompson and Pollard*, 1995a, 1995b], used within IBIS for describing the land surface processes, does not represent the dynamics of water table physically. In the LSX the bottom boundary condition of soil is specified as the unsaturated conductivity of the lowest layer multiplied by an empirical drainage coefficient ranging from 0 to 1, where 0 is a no-flux condition such as impermeable bedrock and 1 is a gravity drainage condition. Since this coefficient controls the drainage rate out of the soil column, it has an important impact on partitioning of rainfall between runoff and evapotranspiration. However, it is impossible to estimate the coefficient in the field since it is not physically based. Similar to LSX most current land surface models do not include a representation for the groundwater table [*Yeh*, 2003]. Therefore the land surface models apply a gravitational drainage condition or linear function of gravity drainage condition with an empirical coefficient which accounts for the other factors affecting soil drainage such as the location of bedrock or groundwater table [*Boone and Wetzel*, 1996].

[42] Since it is difficult to include a detailed groundwater dynamics in a land surface model, we represent the groundwater table as a lower boundary for the soil column. From experiments using SHE we obtain a reasonable estimate of the annual cycle of spatially variable location of the GWT corresponding to the same rainfall forcing. Valley areas have shallow groundwater table depths that fluctuate following storm events. Hill areas have deep water table depths that are less sensitive to storm events than valley areas. Therefore the bottom boundary of IBIS can be specified with the cycle of groundwater table corresponding to the different topographic characteristics. We will see whether the IBIS simulations result in different or same equilibrium vegetation (forests or grasslands) corresponding to the differently specified GWT at each region. If the IBIS could simulate forests and grasslands respectively in each

run with different cycles of GWT at the same latitude, we would conclude that IBIS-SHE simulates the savanna ecosystem. We expect the areas with a shallow (deep) water table might have forest (grassland) as equilibrium only in natural savannas. In order to include the GWT as a boundary the soil model of IBIS is modified.

[43] In simulations using SHE the model assumes homogeneous atmospheric conditions and homogeneous soil properties over the domain. The redistribution of soil moisture is a direct response to topography. A small representative catchment (~820 km²) is delineated from GTOPO30 in the Republic of Niger. This elevation field is used to generate the annual cycle of GWT in response to the observed topographic variations for all the experimental cases of 9°, 11°, and 13°N. The GWT is assumed to be at the surface at the initial time. The simulations are repeated with the annual cycles of daily atmospheric conditions (rainfall intensity and potential evaporation) until hydrologic variables, such as the depth to GWT, reach equilibrium regardless of the initial arbitrary conditions. The resulting seasonal cycle of GWT is then used to drive the modified IBIS including GWT as a lower boundary condition.

[44] The groundwater table depth is simulated assuming bare soil conditions. This assumption may not be fully justified since the existence of vegetation would impact the annual cycle of water table depth. However, this assumption may not be extremely limiting since our objective here is to understand the role of water table depth in dictating the vegetation type and not to explore the full range of interactions between vegetation and the GWT.

[45] Except for adding the GWT, all other conditions are the same as the former set in experiment 1. However, the results from the region at 9°N, where savannas are observed but forests are simulated using IBIS, are not presented here. In the previous set of experiments the bottom of the soil column is assumed to have free gravitational drainage condition. Despite that assumption, IBIS simulates a dry forest at 9°N, where savanna ecosystem is observed in reality. Adding a water table boundary condition should make the soil moister and hence should not result in a transition to grass. Therefore the simulations at 9°N result in dry forest regardless of the depth of the GWT.

6.2. Results
6.2.1. Results at 11°N

[46] From simulations using SHE we have various cycles of groundwater table levels that correspond to the different topographic settings. We also note that as the water table depth becomes shallower, it becomes more sensitive to fluctuations in the atmospheric forcing such as rainfall (see Figure 9).

[47] At 11°N the biospheric model simulates grasslands under the normal condition. We expect that a shallow water table might create a niche for trees to dominate over a fraction of this region. We used different cycles of water table generated with SHE, which is a response to its surrounding topographic settings, to see if we can simulate a transition from grass to trees (see Figure 10). Using the annual cycle of water table depth at location A (where the annual mean depth to GWT is ~2.5 m) as a boundary, grasslands are simulated. The lower canopy LAI at location A stays around 6.5, and the upper canopy LAI is quite small. On the other hand, at location B (where the annual
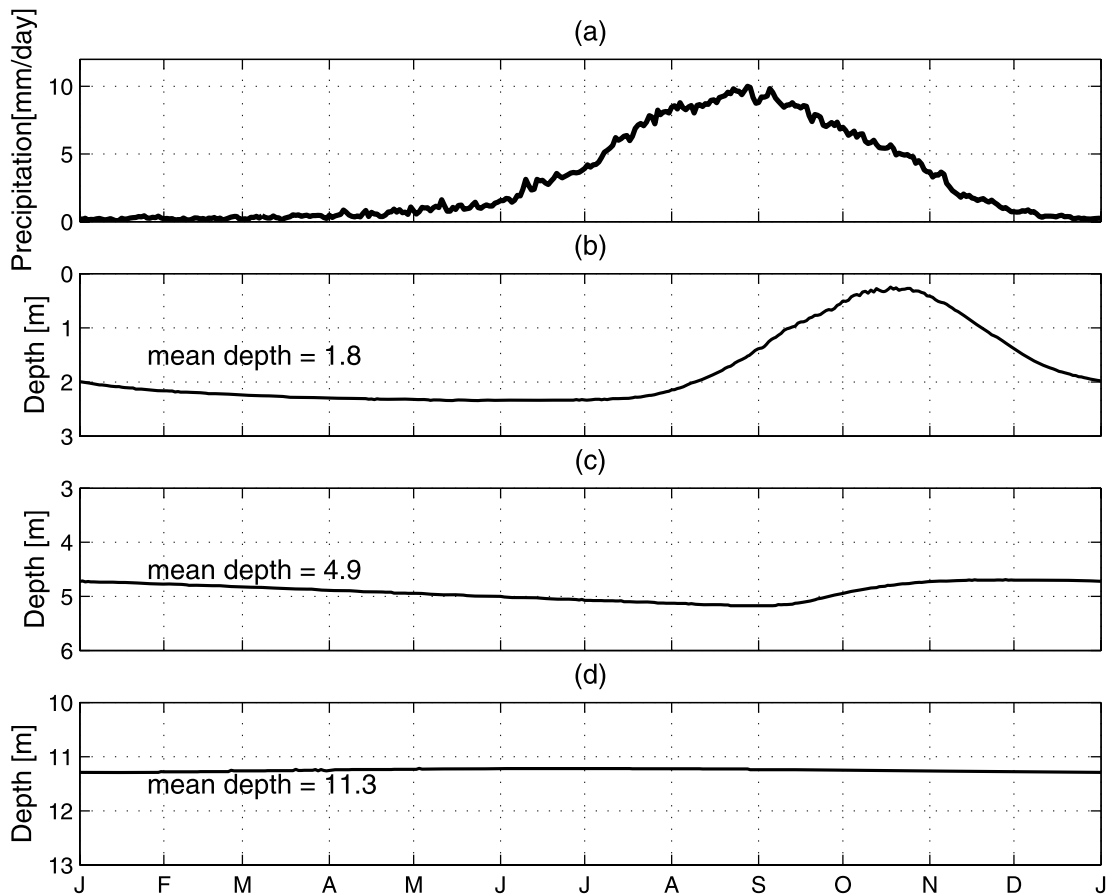
Figure 9. At 11°N, (a) annual cycle of precipitation and (b–d) groundwater table depth. The different topographic settings show the various cycle of groundwater table.

mean depth to GWT is ~2.3 m), having shallower GWT than location A, the upper canopy LAI evolves to around 3 after 350 years. Location B is dominated by deciduous tropical trees. As a result, forests are simulated when GWT is at ~2.5 m, but grasslands are simulated when GWT is deeper than 2.5 m. The fraction of the area dominated by trees, with an annual mean groundwater table depth smaller than 2.5 m, is ~8%.

6.2.2. Results at 13°N

[48] At 13°N the model simulates grasslands under the normal atmospheric condition with the assumption of free drainage condition at the bottom of the soil column. In nature this area is dominated by grass. With either of the forcings from NCEP/NCAR or HAPEX-Sahel, grasslands are simulated even when assuming the shallowest water table depth from SHE simulations. It suggests that all the grids of SHE in 13°N are dominated by grasses. Trees would not succeed in the competition within this model even when the capillary fringe of the GWT reaches the surface.

[49] In addition, the annual cycle of GWT in the NCEP/NCAR simulations is more stable than that of HAPEX-Sahel simulations. This is attributable to the characteristics of storm events, which are less intense and more frequent in NCEP/NCAR, as seen in Figure 6.

6.3. Summary

[50] Using asynchronous coupling of SHE and IBIS, at 11°N, the model simulates deciduous trees over a shallow

water table depth and grasses over a deep water table depth. The estimated area covered by deciduous trees is ~8% of total area. A region can be defined as savannas with the tree canopy covering more than 5% and <80% of the land surface [*Scholes and Walker*, 1993]. Hence the simulation results are consistent with the savanna ecosystems at 11°N. At 13°N, grasslands dominate in the simulations regardless of water table depth, which is consistent with the observation that grasslands dominate this region. Therefore the results of these experiments demonstrate that topographically induced variability of water table depth and soil moisture facilitates coexistence of trees and grasses under atmospheric climate characteristic of savanna.

7. Discussion and Conclusion

[51] This paper has addressed the question of how savannas emerge in general. Savannas can be shaped by many factors: fires and interannual variability of rainfall (disequilibrium theory) and existence of different niches in vertical profile of soil water shared by trees and grasses (equilibrium theory). In this study, it is hypothesized that a mixture of trees and grasses can exist owing to the variability of soil moisture that naturally results from variability in topography. Specifically, we hypothesize that "variations in elevation at relatively short horizontal scales (~1 km) force similar variations in soil moisture and thus create significantly different hydrologic niches within any large area.
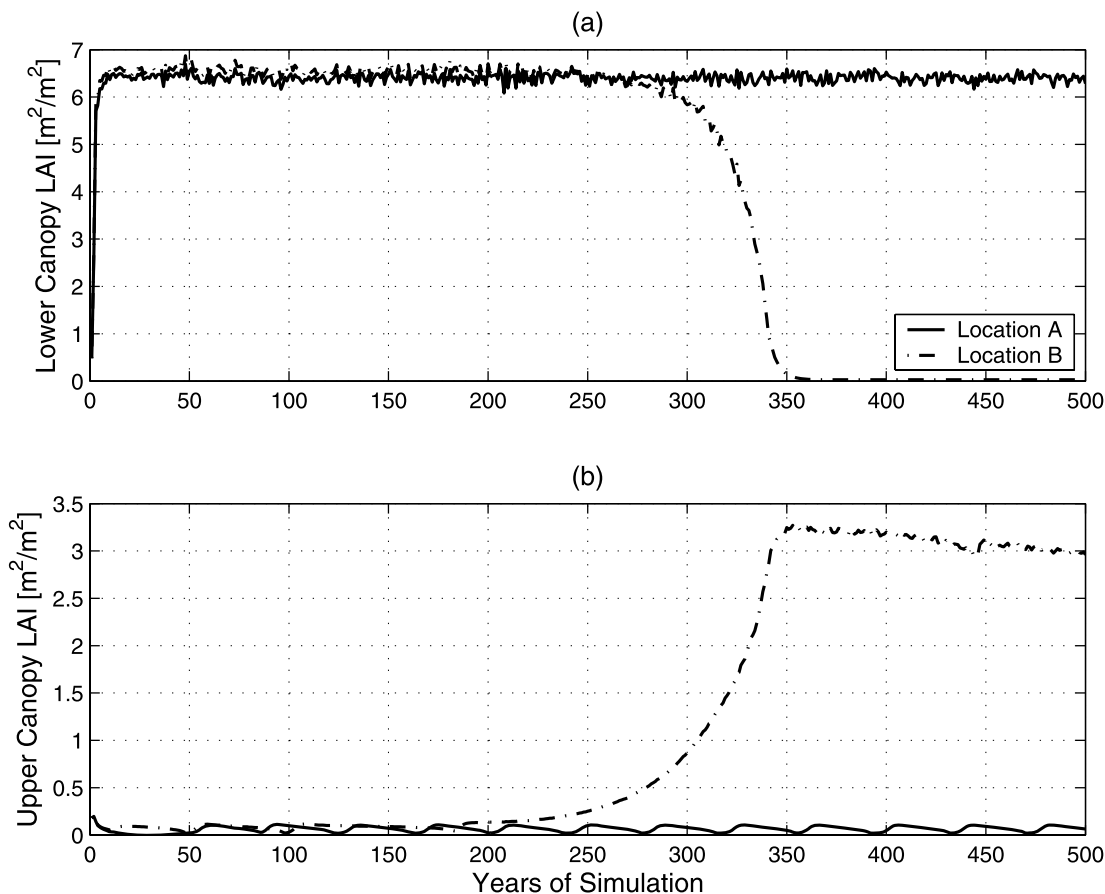
Figure 10. At 11°N, change of the leaf area index (LAI) of (a) lower canopy and (b) upper canopy during the simulation in location A (annual mean depth to GWT is 2.5 m, solid line) and location B (annual mean depth to GWT is 2.3 m, dash-dotted line). The different location in the same catchment can have different types of vegetation, grass or tree, only in savannas.

Under water-limited conditions the relatively wet valleys favor trees, while the relatively dry hills favor grasses. This coexistence of trees and grasses is only possible for a window of climatic conditions that is characteristic of savannas.'' This hypothesis has been tested using the biosphere model (IBIS) only and asynchronous coupling of the biospheric model (IBIS) and a distributed hydrologic model (SHE).

[52] In the two sets of experiments we simulate different types of vegetation in response to different water conditions only in natural savannas, not in natural grasslands (see Table 1). In the first set of experiments the different water conditions are simulated by prescribing different magnitudes of the rainfall forcing. In the second set of experiments the different water conditions are simulated by prescribing different water table depths. The spatial variation of water availability in the horizontal is shown to facilitate coexistence of trees and grasses in savannas. Both results suggest that the variability of soil moisture forced by topography can be a determinant factor of vegetation distribution within savannas. Further, they confirm that this role of topography can be significant only in a certain climatic window characteristic of savannas.

[53] In the first set of experiments, prescribed forcing of around 1000 and 2000 mm of annual rainfall defines the grass/tree transition at 9° and 11°N, respectively. These amounts are quite different, although both regions fall into savannas. This result suggests that other meteorological inputs such as air temperature and solar radiation (refer to Figure 4) perhaps play important roles and demonstrates that water is not the only one determinant factor in savannas. Moreover, at 13°N, grassland is simulated even when very high rainfall is assumed. The experiments at 13°N only simulate grasslands as equilibrium ecosystems. We observe grasslands in nature. Even with more than 3500 mm of the annual accumulated rainfall, only grasses are simulated in the model. This amount of rainfall is enough to support forests in the areas of 9° and 11°N.

[54] In the second set of experiments, by using SHE and IBIS asynchronously, the model simulates trees at 9°N, even when the GWT is assumed to be infinitely deep; at 13°N the model simulates grasses even when the capillary fringe of

Table 1. Summarized Results

	Latitude, °N		
	9	11	13
Observation	savannas	savannas	grasslands
IBIS	forests	grasslands	grasslands
Asynchronous coupling of IBIS and SHE	forests	savannas	grasslands

the GWT reaches the surface. However, for the transitional climate, at 11°N, trees are simulated when the GWT is at ~2.5 m from the surface, but grasses are simulated when the GWT is deeper than 2.5 m. Trees are not simulated at 13°N even with the shallowest water table depth. It suggests that other meteorological conditions may limit this region and make it impossible to support trees. Figure 4 shows that the area at 13°N is under more severe environments for plants with higher temperature, less relative humidity, and less cloud cover compared to other regions. These factors perhaps prevent the growth of woody plants.

[55] In this study, we only include grasslands and savannas for the experimental simulations, but not forests, the southern limit of savannas. In the moist forest of the southern subregion of West Africa the water availability does not limit the plant growth. Rather, solar energy availability does, owing to the existence of clouds [*Wang and Eltahir*, 2000b]. The coastal area near the Atlantic Ocean receives plenty of moisture supply which would ease the local water deficit that may arise owing to topographic conditions. Therefore the modification of available water through any input (rainfall amount or GWT) has not been applied to investigate the plant growth in the coastal forest ecosystem using IBIS. On the other hand, the water-limited grasslands and savannas cannot easily rebound from the certain range of modification in water availability. As a result the change in water availability can affect the growth of plants.

[56] The stated hypothesis suggests that a mixture of trees and grasses may coexist in response to the variation of topography in natural savannas. A model that can fully describe the complex distributed hydrologic processes including the dynamics of vegetation is required to test the proposed hypothesis. However, the availability of such models is limited, although a few models such as Topog-IRM [*Vertessy et al.*, 1996] and Regional Hydro-Ecologic Simulation System (RHESSys) [*Mackay and Band*, 1997; *Mackay*, 2001] have been developed. The ecohydrological models often combine the biogeochemical and hydrological components to predict the spatial distribution of the fluxes of energy, water, carbon (plant growth), and nutrients (e.g., nitrogen). However, the models listed above concentrate on the biogeochemical processes to estimate the vegetation productivity (ecosystem function) instead of simulating the biogeographic responses to climate (ecosystem structure) and thus predicting the local dominance of vegetation types [*Mello et al.*, 2001]. As a consequence it was essential in our study to implement a scheme that simulates plant competition for available resources such as IBIS. The development of fully coupled distributed model will help in better understanding the interplay between soil moisture and vegetation dynamics as well as in additional testing of the hypotheses on emergence of savanna.

References

Abbott, M. B., J. C. Bathurst, P. E. O'Connel, and J. Rasmussen (1986a), An introduction to the European Hydrological System—Systeme Hydrologique Europeen "SHE," 1: History and philosophy of a physically-based distributed modelling system, *J. Hydrol.*, 87, 45–59.

Abbott, M. B., J. C. Bathurst, P. E. O'Connel, and J. Rasmussen (1986b), An introduction to the European Hydrological System—Systeme Hydrologique Europeen "SHE," 2: Structure of a physically-based distributed modelling system, *J. Hydrol.*, 87, 61–77.

Anderson, J., E. Hardy, J. Roach, and R. Witmer (1976), A land use and land cover classification system for use with remote sensor data, *U.S. Geol. Surv. Prof. Pap.*, 964, 28 pp.

Boone, A., and P. J. Wetzel (1996), Issues related to low resolution modeling of soil moisture: Experience with the PLACE model, *Global Planet. Change*, 13, 161–181.

Bourliere, F., and M. Hadley (1983), *Present-Day Savannas: Overview in Ecosystem of the World—Tropical Savannas*, Elsevier Sci., New York.

Casper, B. B., and R. B. Jackson (1997), Plant competition underground, *Annu. Rev. Ecol. Syst.*, 28, 545–570.

Eagleson, P. S., and R. I. Segarra (1985), Water-limited equilibrium of savanna vegetation systems, *Water Resour. Res.*, 21(10), 1483–1493.

Foley, J. A., C. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Stitch, and A. Haxeltine (1996), An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, *Global Biogeochem. Cycles*, 10(4), 603–628.

Graham, D., and L. Klide (2002), *MIKE SHE User Guide*, DHI Water and Environ., Hørsholm, Denmark.

Jeltsch, F., G. E. Weber, and V. Grimm (2000), Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence, *Plant Ecol.*, 151, 161–171.

Mackay, D. S. (2001), Evaluation of hydrologic equilibrium in a mountainous watershed: Incorporating forest canopy spatial adjustment to soil biogeochemical processes, *Adv. Water Resour.*, 24, 1211–1227.

Mackay, D. S., and L. E. Band (1997), Forest ecosystem processes at the watershed scale: Dynamic coupling of distributed hydrology and canopy growth, *Hydrol. Processes*, 11, 1197–1217.

Mello, J., A. Janetos, D. Schimel, and T. Kittel (2001), *Climate Change Impacts on the United States: The Potential Consequences of Climate Variability and Change: Foundation/A Report of the National Assessment Synthesis Team, US Global Change Research Program*, chap. 2, Cambridge Univ. Press, New York.

Pollard, D., and S. L. Thompson (1995), Use of a land-surface-transfer scheme (LSX) in a global climate model: The response to doubling stomatal resistance, *Global Planet. Change*, 10, 129–161.

Porporato, A., P. D'Odorico, F. Laio, and I. Rodriquez-Iturbe (2003), Hydrologic controls on soil carbon and nitrogen cycles. 1. Modeling scheme, *Adv. Water Resour.*, 26, 45–58.

Rodriguez-Iturbe, I., P. D'Odorico, A. Porporato, and L. Ridolfi (1999), Tree-grass coexistence in savannas: The role of spatial dynamics and climate fluctuations, *Geophys. Res. Lett.*, 26(2), 247–250.

Scholes, R. J., and B. H. Walker (1993), *An African Savanna, Synthesis of the Nylsvley Study*, Cambridge Univ. Press, New York.

Skarpe, C. (1992), Dynamics of savanna ecosystems, *J. Veg. Sci.*, 3, 293–300.

Thompson, S. L., and D. Pollard (1995a), A global climate model (GENESIS) with a land-surface transfer scheme (LSX). Part 1: Present climate simulation, *J. Clim.*, 8, 732–761.

Thompson, S. L., and D. Pollard (1995b), A global climate model (GENESIS) with a land-surface transfer scheme (LSX). Part 2: CO_2 sensitivity, *J. Clim.*, 8, 1104–1121.

Vertessy, R. A., T. J. Hatton, R. G. Benyon, and W. R. Dawes (1996), Long-term growth and water balance predictions for a mountain ash (*Eucalyptus regnans*) forest catchment subject to clear-felling and regeneration, *Tree Physiol.*, 16, 221–232.

Walker, B. H., C. Holling, and R. M. Peterman (1981), Stability of semi-arid savanna grazing systems, *J. Ecol.*, 69(2), 473–498.

Walter, H. (1971), *Ecology of Tropical and Subtropical Vegetation*, Oliver and Boyd, White Plains, N. Y.

Wang, G., and E. A. B. Eltahir (2000a), Biosphere-atmosphere interactions over West Africa. 1: Development and validation of a coupled dynamic model, *Q. J. R. Meteorol. Soc.*, 126, 1239–1260.

Wang, G., and E. A. B. Eltahir (2000b), Biosphere-atmosphere interactions over West Africa. 2: Multiple climate equilibria, *Q. J. R. Meteorol. Soc.*, 126, 1261–1280.

Yeh, P. J. (2003), Representation of water table dynamics in a land surface scheme: Observations, models, and analyses, Ph.D. thesis, Mass. Inst. of Technol., Cambridge.

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