Vegetation–Climate Feedbacks in the Conversion of Tropical Savanna to Grassland

WILLIAM A. HOFFMANN AND ROBERT B. JACKSON*

Department of Botany, The University of Texas at Austin, Austin, Texas

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ABSTRACT

Tropical savannas have been heavily impacted by human activity, with large expanses transformed from a mixture of trees and grasses to open grassland and agriculture. The National Center for Atmospheric Research (NCAR) CCM3 general circulation model, coupled with the NCAR Land Surface Model, was used to simulate the effects of this conversion on regional climate. Conversion of savanna to grassland reduced precipitation by approximately 10% in four of the five savanna regions under study; only the northern African savannas showed no significant decline. Associated with this decline was an increase in the frequency of dry periods within the wet season, a change that could be particularly damaging to shallow-rooted crops. The overall decline in precipitation is almost equally attributable to changes in albedo and roughness length. Conversion to grassland increased mean surface air temperature of all the regions by 0.5°C, primarily because of reductions in surface roughness length. Rooting depth, which decreases dramatically with the conversion of savanna to grassland, contributed little to the overall effect of savanna conversion, but deeper rooting had a small positive effect on latent heat flux with a corresponding reduction in sensible heat flux. The authors propose that the interdependence of climate and vegetation in these regions is manifested as a positive feedback loop in which anthropogenic impacts on savanna vegetation are exacerbated by declines in precipitation.

1. Introduction

It is widely established that climate is a major determinant of vegetation structure and function, but the extent to which vegetation influences climate is far less certain. Because plants are the primary site for the exchange of water, energy, and momentum between the land and atmosphere, vegetation has an important role in the climate system. This role has been particularly well documented in the lowland Tropics, where numerous modeling studies have demonstrated that largescale deforestation may lead to decreased precipitation and increased temperature (Dickinson and Kennedy 1992; Polcher 1995; Zhang and Henderson-Sellers 1996; Lean and Rowntree 1997; Hahmann and Dickinson 1997). In semiarid regions, other modeling studies have determined that overgrazing may result in similar changes in precipitation and temperature (Charney 1975; Sud and Fennessy 1982; Xue and Shukla 1993).

Semiard regions lie a band of tropical savanna, a vegetation type composed of a mixture of trees and grasses. Tropical savannas have been subjected to much pressure from human activities, since nearly one-fifth of the world’s population lives in regions that are currently, or were recently, covered by this vegetation type (Solbrig et al. 1996). Humans have increased the frequency of fire, primarily in moist tropical savannas where burning now typically occurs at intervals of 1–3 yr (Lacey et al. 1982; Trollope 1984; Coutinho 1990; Stott 1990; Menaut et al. 1991; Russell-Smith et al. 1997), a rate that can greatly reduce savanna tree densities (Hoffmann 1999). Dominant land use in these moist savannas is varied, ranging from mostly beef cattle production in northern Australia (Winter 1990), cattle production and large-scale agriculture in Brazil (Klink et al. 1995), and mixed grazing and shifting and permanent cultivation in Africa. In many cases, the conversion to agriculture and pasture has been rapid. For example, approximately 40% of the Brazilian cerrado has been converted to these uses, and the remaining area is being transformed at a rate of 1.7% per year (Klink et al. 1995). In some regions, harvesting of trees for firewood and charcoal is another important activity reducing tree density (Monela et al. 1993). The net result of these activities is the conversion of a tree–grass mixture to a vegetation dominated by grasses and other herbaceous plants, including crops.

A reduction in woody cover can have important ef-
fects on the physical properties of tropical savanna. Savannas have lower albedo than do grasslands (Oguntoyinbo 1970) as well as higher surface roughness (Miranda et al. 1997) and greater rooting depth (Jackson et al. 1997), all of which influence land–atmosphere interactions. Of primary importance is albedo, which has been shown to be the principle parameter determining the effects of tropical deforestation on precipitation (Dirmeyer and Shukla 1994; Hahmann and Dickinson 1997). As proposed by Charney (1975), an increase in albedo can reduce convection by reducing heat flux into the lower atmosphere, thus inhibiting the primary mechanism generating precipitation in the Tropics.

The reduction in roughness length may also have considerable impact on precipitation and surface temperature. Surface temperature increases because of reduced conduction of sensible and latent heat from the surface to the atmosphere. The reduced heat flux into the atmosphere can reduce convection, thus reducing precipitation. However, roughness length can have significant effects on large-scale circulation patterns, making it difficult to predict the changes in precipitation. While some deforestation simulations have demonstrated that decreased roughness length results in lower precipitation (Pitman et al. 1993; Hahmann and Dickinson 1997), others have not (Zeng et al. 1996; Lean and Rowntree 1997).

In this study, the climatic effects of transforming savanna to grassland are simulated with a general circulation model, with primary focus on moist tropical savanna. Dry savanna (i.e., less than 600–700 mm annual rainfall) is also being subjected to intense human pressure, but the land surface changes often differ substantially from the changes discussed here. In many dry savannas, as well as many temperate savannas and grasslands, woody plants are encroaching rather than declining (Jackson et al. 2000).

2. Model description

Simulations were run using the National Center for Atmospheric Research (NCAR) Community Climate Model (CCM3). CCM3 has a spatial resolution of approximately 2.8° × 2.8° of the earth’s surface (T42 spectral truncation) and 18 vertical levels. The vertical dimension is represented with a hybrid sigma-pressure coordinate system. A detailed model description is available from Kiehl et al. (1998). CCM3 is coupled with the NCAR Land Surface Model (LSM) described by Bonan (1996). LSM simulates the fluxes of momentum, radiation, latent heat, and sensible heat between the land and the atmosphere. An analysis of the control climatology of CCM3–LSM is presented by Bonan (1998).

Within LSM, each grid cell of the vegetated surface of the earth is assigned one of 28 vegetation types. Each vegetation type is composed of bare soil and one or more plant types. For example, tropical savanna vegetation is composed of subgrid patches of bare soil, tropical seasonal trees, and C₃ grass. A total of 12 plant types are represented in LSM, differing in leaf area, stem area, root profile, leaf dimension, optical properties, stomatal physiology, roughness length, and displacement height. The default parameter values defining these characteristics were used (Table 1), except for the empirical parameter β (vertical root distribution), which was obtained from the recent database of Jackson et al. (1997). This unitless parameter is defined by the relation \( Y = 1 - \beta^d \), where \( Y \) is the cumulative root fraction from the soil surface to depth \( d \) (cm).

Within a grid cell, albedo is not prescribed as a single parameter. Rather, it is calculated from the optical properties of the relevant plant types and from the color and moisture content of the underlying soil using a two-stream canopy reflectance model (Bonan 1996).

Five tropical savanna regions were the focus of this study: 1) the cerrado of Brazil, 2) the llanos of northern South America, 3) the southern African savannas, 4) the northern African savannas, and 5) the savannas of northern Australia. The default LSM vegetation map was used, except for South America, where some modification was necessary so that the distribution of the savanna vegetation type would correspond well to the actual distribution of moist tropical savanna (Fig. 1). The distribution of savanna in Brazil was modified to conform to the vegetation map of the Instituto Brasileiro de Geografia e Estatística (IBGE 1993). Savannas of the llanos of Colombia and Venezuela were modified according to the United Nations Educational, Scientific and Cultural Organization Vegetation Map of South America (UNESCO 1980). To exclude dry savannas from the simulations, savannas of northeastern Brazil (caatinga) and Paraguay and northern Argentina (chaco) were not included in the savanna vegetation class. The distribution of savanna in the default LSM vegetation map corresponds quite well to the actual distribution of moist savanna in Africa and Australia (Nix 1983) so no modifications were performed in these continents.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Tropical seasonal tree</th>
<th>C₃ grass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rooting parameter</td>
<td>0.982</td>
<td>0.943</td>
</tr>
<tr>
<td>Roughness length (m)</td>
<td>0.99</td>
<td>0.06</td>
</tr>
<tr>
<td>Displacement height (m)</td>
<td>12.06</td>
<td>0.34</td>
</tr>
<tr>
<td>Top of canopy (m)</td>
<td>18.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Bottom of canopy (m)</td>
<td>10.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Mean leaf area index*</td>
<td>1.2</td>
<td>1.1</td>
</tr>
<tr>
<td>Mean stem area index**</td>
<td>0.5</td>
<td>0.64</td>
</tr>
</tbody>
</table>

* Leaf area index and stem area index vary throughout the year according to a prescribed phenology. Only mean annual values are given here.
3. Simulations

Climate was simulated under two scenarios. The “savanna” scenario represents the unmodified vegetation, composed of a mixture of trees and grasses. The “grassland” scenario corresponds to a modified landscape dominated by grassland. In the latter scenario, all savanna was converted to grassland, representing an extreme case of complete transformation of this vegetation.

The proportional cover of trees and grass is determined by parameters within LSM. Prescribing a single tree density for the savanna scenario is a difficult endeavor, considering that savanna vegetation is extremely variable, ranging from open grassland to woodland with a nearly closed tree canopy. Furthermore, humans have had considerable impact on savannas for thousands of years, making it impossible to define an “undisturbed” or “original” state. Here we use 50% tree cover as the original tree density, which in LSM corresponds to a mean projected tree canopy cover of 34% during the summer months. This probably underestimates the original tree density in the southern African savannas, where relatively dense Miondo woodlands predominate (Menaut 1983) and corresponds quite well to observed canopy cover in the northern Australian savannas (Walker and Gillison 1982). It may overestimate tree cover in the Brazilian cerrado, where Goodland and Ferri (1979) observed a mean projected canopy cover of 19% in a large sample of typical savanna sites. However, the latter measurements were taken in the dry season when canopy cover is reduced and included sites subjected to frequent burning, so the natural tree cover may have been considerably higher.

Because of the importance of albedo in land-atmosphere interactions, it is essential that the scenarios generate realistic albedo values within LSM. Over the tropical savannas regions, the savanna scenario had a mean albedo of 0.157, while the grassland scenario had a mean albedo of 0.194. These values compare quite closely to the mean annual values of 0.149 and 0.195, which were measured by Oguntoyinbo (1970) in savanna and grassland in the Guinean zone of Nigeria. Similarly, Mathew’s (1983) dataset provides mean annual values of 0.153 and 0.185. In short, the simulated increase in albedo was 0.037, as compared to 0.046 from Oguntoyinbo (1970) and 0.032 from Matthews (1983).

Each scenario consisted of an initial 15-month model run, which was discarded as a spinup to the actual simulation, which was run for 8 additional yr. Simulations were run with climatological monthly mean sea surface temperatures.

In addition to the scenarios described above, sensitivity analyses were performed to quantify the contributions of albedo, roughness length, and rooting depth to the overall change in climate. Each of these factors was examined in a separate simulation by modifying the attributes of the tropical seasonal tree functional type. These simulations were identical to the savanna scenario, except that certain parameters of the tropical seasonal tree functional type were changed to the corresponding parameters for C4 grass. Modifying the characteristics of the tropical seasonal tree functional type
has no effect on nonsavanna regions, since this functional type is not included in any other vegetation present on the LSM vegetation map. Table 1 lists the parameters that were modified for each analysis. Since the sensitivity runs were expected to be relatively similar to the savanna scenario, each simulation was begun as a branch run from the 10th month of the savanna simulation. The first 5 months of the new simulation was discarded, and the simulation was run for an additional 5 yr. In short, the spinup was composed of a 10-month control run, followed by a 5-month sensitivity run.

4. Statistical analyses

The $t$ test was employed to determine the statistical significance of converting savanna to grassland. Comparisons were performed for each of the five major savanna regions described above. Additional isolated grid cells of tropical savanna are distributed throughout the Tropics, but these were omitted from all comparisons.

Within each savanna region, monthly values of each output variable were averaged over all grid cells to obtain a single monthly mean. All statistical tests were performed on these regional monthly means, so the problem of spatial autocorrelation was avoided. Variances were calculated from monthly anomalies, which were obtained by subtracting each monthly value from the multyear mean for that month. Calculating variances from these anomalies requires an adjustment to the degrees of freedom, because one degree of freedom is lost for each monthly mean calculated. Therefore, these variances have $12(n - 1)$ degrees of freedom, where $n$ is the number of years.

Most variables were found to have significant positive temporal autocorrelation in the monthly anomalies. To correct the $t$ test for the nonindependence of the monthly anomalies, the sample size was adjusted, as described by Zwiers and von Storch (1995). The equivalent sample size is $n_e = n(1 - r)/(1 + r)$, where $n$ is the sample size, and $r$ is the autocorrelation between consecutive monthly anomalies. This $n_e$ was used as the sample size for calculating the standard errors in the $t$ test.

5. Effects of savanna conversion on climate

a. Mean climate

In the control simulations, mean annual precipitation ranged from 928 mm yr$^{-1}$ in the Australian savannas to 1790 mm yr$^{-1}$ in the llanos. Changing woody plant cover from 50% to 0% resulted in a significant decline in precipitation in all savanna regions except northern Africa (Fig. 2, Table 2). For the four regions exhibiting a significant change, mean annual precipitation declined by 8%–13%. Mean annual evapotranspiration was reduced in every region by 8%–10%, even in the northern African savannas, where precipitation was virtually unaffected (Table 2). This suggests that moisture availability was not the primary factor driving the decline in evapotranspiration. Instead, reductions in available
energy, rooting depth, and conductance appear to be the primary cause of the reduced evapotranspiration.

In every case except northern Africa, precipitation declined more than did evapotranspiration, indicating a reduction in moisture convergence (Table 2). Moisture convergence, that is, the net flux of water vapor into a region, has similarly been found to decline in most tropical deforestation simulations (Hahmann and Dickinson 1997). This reduction in moisture convergence must be compensated by an equivalent change in runoff, provided that changes in water storage are small. These simulations were sufficiently long relative to the change in soil moisture storage, so the change in runoff was similar to the change in moisture convergence (data not shown). The llanos, the cerrado, and northern Australia all experienced decreases in runoff of 50–60 mm yr⁻¹.

Conversion of savanna to grassland increased mean annual surface air temperature by 0.4°–1.0°C over most of the area occupied by tropical savanna (Fig. 3). Mean annual net solar radiation absorbed at the surface declined by 5.5 W m⁻² over the five regions, but this decline varied among the regions (Table 3). This decrease in absorbed solar radiation was considerably less than the 9.2 W m⁻² expected solely due to the increase in albedo if incident solar radiation were unchanged. However, such a large decrease in net solar radiation was not realized because of an increase in incident solar radiation, primarily due to a reduction in fractional cloud cover by 0.015 (Table 4).

Net upward longwave radiation, which is upward longwave radiation minus downward longwave radiation, increased by 3.9 W m⁻² (Table 3). This was due primarily to a 3.1 W m⁻² increase in longwave radiation emitted from the surface, resulting from increased surface temperature. However, the downward flux of longwave radiation also declined by 0.8 W m⁻², thus contributing to the overall increase in net upward longwave radiation. The decline in the downward flux of longwave radiation is likely a result of reduced cloud cover.

Because of the changes in longwave radiation and incident solar radiation, net radiation decreased by 9.4 W m⁻² in response to vegetation change. The reduction in net radiation represents a reduction in the energy available for latent and sensible heat flux. Thus, latent heat flux declined by 6.3 W m⁻² and sensible heat flux declined by 3.0 W m⁻² (Table 3).

### b. Seasonal patterns

In the moist tropical savannas, where precipitation is abundant for a large fraction of the year, changes in seasonal patterns of rainfall may be more important than an overall reduction in mean annual precipitation. In these simulations, precipitation was reduced throughout the wet season, with no consistent change in the seasonality of rainfall (Fig. 4). However, it is important to note that in all cases except the northern African savannas, there were large declines in precipitation in months near the beginning or end of the dry season. The presence or absence of rainfall at these times can effectively determine the length of the dry season, so the reduction in precipitation would result in a lengthening of the dry season.

In the llanos of northern South America, conversion to grassland resulted in a depression in precipitation during the middle of the wet season. This is a magnification of a phenomenon that is quite common in both the cerrado and the llanos, and perhaps the other savanna regions. In these savannas, there are commonly periods of drought lasting one to several weeks during the middle of the wet season. These dry periods can have considerable impact on shallow-rooted crops (Cochrane et al. 1988). The timing of such dry periods is quite variable, so mean monthly precipitation does not typically reveal a decline in midsummer, as is often observed in more tropical climates. An increase in the frequency or length of these dry periods could be responsible for the bimodal distribution of rainfall. Even in regions where savanna transformation did not result in such a dramatic decline in summer precipitation, there may still be an increase in the frequency of dry periods at this time. An increase in the frequency of such periods will likely depend on whether the precipitation decline is manifested as a decline in the frequency of convective events or a decline in the average intensity of each convective event. Polcher (1995), in a GCM study, found that trop-
Change in Surface Temperature (°C)

Fig. 3. Change in mean annual surface air temperature resulting from conversion of tropical savanna to grassland. All five savanna regions exhibited a significant increase in surface air temperature. Savanna regions are outlined.

Table 3. Changes in the mean annual surface energy budget resulting from the conversion of savanna to grassland.

<table>
<thead>
<tr>
<th>Region</th>
<th>Net downward shortwave flux (W m⁻²)</th>
<th>Net upward longwave flux (W m⁻²)</th>
<th>Sensible heat flux (W m⁻²)</th>
<th>Latent heat flux (W m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Change</td>
<td>Control</td>
<td>Change</td>
</tr>
<tr>
<td>Cerrado</td>
<td>203.6</td>
<td>-2.4⁺</td>
<td>73.0</td>
<td>+5.2⁺</td>
</tr>
<tr>
<td>Llanos</td>
<td>219.4</td>
<td>-1.5⁺</td>
<td>59.8</td>
<td>+4.7⁺</td>
</tr>
<tr>
<td>Northern Africa</td>
<td>219.1</td>
<td>-5.9⁺</td>
<td>57.8</td>
<td>+3.9⁺</td>
</tr>
<tr>
<td>Southern Africa</td>
<td>208.8</td>
<td>-6.1⁺</td>
<td>79.7</td>
<td>+3.6⁺</td>
</tr>
<tr>
<td>Australia</td>
<td>205.7</td>
<td>-5.8⁺</td>
<td>78.7</td>
<td>+2.6⁺</td>
</tr>
</tbody>
</table>

* Not significant.
⁺ 0.05 > P > 0.01.
⁺⁺ 0.01 > P > 0.005.
⁺⁺⁺ P < 0.005.
TABLE 4. Effects of tropical savanna transformation on mean annual values of three variables.

<table>
<thead>
<tr>
<th>Region</th>
<th>Albedo</th>
<th>Temperature (°C)</th>
<th>Fractional cloud cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cerrado</td>
<td>+0.034*</td>
<td>+0.73*</td>
<td>-0.020*</td>
</tr>
<tr>
<td>Llanos</td>
<td>+0.032*</td>
<td>+0.76*</td>
<td>-0.016*</td>
</tr>
<tr>
<td>Southern Africa</td>
<td>+0.038†</td>
<td>+0.55†</td>
<td>-0.010†</td>
</tr>
<tr>
<td>Australia</td>
<td>+0.038*</td>
<td>+0.52*</td>
<td>-0.020*</td>
</tr>
</tbody>
</table>

* Not significant.
† 0.05 > P > 0.01.
‡ 0.01 > P > 0.005.
§ P < 0.005.

In deforestation scenarios, where albedo is found to be most responsible for the decline in precipitation (Dirnmeyer and Shukla 1994; Hahmann and Dickinson 1997). In the present study, albedo was reduced by 0.036, considerably less than the prescribed changes in deforestation studies, where albedo is typically reduced by 0.05 to 0.08.

In these simulations, the reduction in roughness length was moderate, yet it had a substantial negative effect on precipitation. The effect of roughness length on precipitation was similar in magnitude and direction to the effect of albedo on precipitation. This contrasts to tropical deforestation studies that have found reductions in roughness length to have small or positive effects on precipitation (Zeng et al. 1996; Lean and Rowntree 1997). However, others have found a substantial negative effect of surface roughness on precipitation (Sad et al. 1988; Hahmann and Dickinson 1997).

Using aggregation rules for area-averaged roughness length (Shuttleworth et al. 1997), we can obtain an estimate for savanna roughness length over the tree, grass, and bare-soil subgrid patches. Using a blending height of 60 m as suggested by Shuttleworth et al. (1997) for CCM3, the mean roughness length is 0.448. The value of 0.448 m for roughness length of savanna is probably unrealistically small. Miranda et al. (1997) determined a roughness length of 1.2 for a Brazilian cerrado savanna with a canopy height of 9 m. This discrepancy is understandable, considering that small-scale interdispersion of trees and grass should result in a rougher canopy than the separation of grasses and trees into separate subgrid patches, as in LSM. Since these simulations used an unrealistically small change in roughness length, the actual change in precipitation was probably underestimated.

To determine the effect of a more realistic roughness length, additional sensitivity analyses were performed to test the effect of increased roughness length, relative to the grassland scenario. The grassland scenario was modified to have roughness length of 1.2, zero plane displacement of 6.3 m, and canopy height of 9 m, to correspond to the values found by Miranda et al. (1997). A second simulation was run with these values doubled. The effects of increasing roughness length are shown in Fig. 6. This curvilinear relationship contrasts to the linear response of precipitation to albedo, as shown by Dirnmeyer and Shukla (1994). However, a curvilinear relationship should be expected for roughness length, since surface stress and surface conductance are approximately linear functions of the logarithm of roughness length.
Reduced roughness length caused a shift in the geographical distribution of precipitation. Precipitation declined near the equator but increased farther from the equator (Fig. 7), as was observed by Hahmann and Dickinson (1997) in their Amazonian deforestation study. With further increases, the point of greatest decline shifted closer to the equator at approximately 10° latitude (data not shown).

Increased rooting depth had little effect on precipitation but caused a small increase in latent heat flux, with a corresponding decline in sensible heat flux. However, the fixed phenology scheme within LSM may limit the effect that changes in rooting depth can have on climate. In dry periods, deep-rooted plants are typically able to retain leaves longer because of the access to deep soil water (Jackson et al. 2000). Longer leaf display would result in greater evapotranspiration and reduced albedo. However, since phenology is fixed within each vegetation type, these consequences of rooting depth do not contribute to the sensitivity analysis.

### Table 5: Results of sensitivity analyses. Values are annual means weighted across the five savanna regions.

<table>
<thead>
<tr>
<th></th>
<th>Overall effect</th>
<th>Albedo effect</th>
<th>Roughness effect</th>
<th>Rooting depth effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precipitation (mm yr⁻¹)</td>
<td>-83.0</td>
<td>-71.0</td>
<td>-67.8</td>
<td>+29.1</td>
</tr>
<tr>
<td>Temperature (K)</td>
<td>+0.58</td>
<td>-0.06</td>
<td>+0.53</td>
<td>+0.21</td>
</tr>
<tr>
<td>Latent heat flux (W m⁻²)</td>
<td>-6.36</td>
<td>-3.01</td>
<td>-1.21</td>
<td>-1.68</td>
</tr>
<tr>
<td>Sensible heat flux (W m⁻²)</td>
<td>-2.63</td>
<td>-5.87</td>
<td>-0.72</td>
<td>+1.79</td>
</tr>
<tr>
<td>Net radiation (W m⁻²)</td>
<td>-8.95</td>
<td>-8.74</td>
<td>-1.95</td>
<td>+0.17</td>
</tr>
</tbody>
</table>

### Figure 7: The change in the latitudinal distribution of precipitation in the savanna regions resulting from a reduction in roughness length from 0.448 to 0.060. Savanna grid cells from the Northern and Southern Hemispheres were pooled to obtain a single mean for each latitude.
savanna regions, most importantly by reducing precipitation and increasing temperature. In four of the five savanna regions, simulated precipitation declined by approximately 10% following the conversion of savanna to grassland. In an environment where water availability seasonally constrains agriculture and ecosystem primary productivity, such a reduction in precipitation may have considerable ecological and economic consequences. However, this decline in annual precipitation offers an incomplete picture of the nature of the climate change. Both spatial and seasonal variation must be considered to understand the full impact of climate change.

The decline in precipitation resulting from the conversion of savanna to grassland was characterized by much spatial variability within each of the savanna regions. Within every region there were areas where precipitation declined by considerably more than 10% (Fig. 2). While some of this variability is undoubtedly caused by the stochastic nature of GCM output, it is likely that some of this variation represents real, consistent differences in climate change. If so, it is necessary to consider the impact on the regions experiencing the greatest declines in precipitation. It is these areas that will experience the greatest economic and environmental impact of the climate change.

Similarly, changes in the seasonal patterns of precipitation may have effects that are not revealed by a mean decline in precipitation. Although precipitation tended to be reduced throughout the entire wet season, with no consistent change in the seasonal distribution of rainfall, this overall decline in precipitation would effectively lengthen the dry season by decreasing the frequency of rainfall at the beginning and end of the wet season. It can be expected that a lengthening of the dry season would increase the probability and intensity of fire (Gill et al. 1996). Fire is the primary form of disturbance in many savannas, and any increase in its frequency would have a negative effect on tree density. In addition, a reduction in the length of the wet season can be expected to reduce primary productivity.

Even changes in wet season precipitation can have important impacts on ecological processes. Seedling establishment can be very sensitive to short dry periods within the wet season (Hoffmann 1996; Klink 1996). This study indicates that these dry periods may become more frequent following the conversion of savanna to grassland, a change that would have a negative impact on tree regeneration. These proposed negative effects on tree density would exacerbate the direct effects of humans on savanna vegetation. A reduction in precipitation brought about by anthropogenic vegetation change should drive further reductions in tree cover, as well as slow the succession of grassland to savanna. Thus any direct effect of humans on the savanna environment would be accelerated because of climatic feedbacks, as has been proposed for semiarid regions susceptible to desertification (Charnay 1975). In the moist savanna regions it is unlikely that the feedbacks would be strong enough to cause desertification, but they could cause a shift in the distribution of biomes. Anthropogenic vegetation change in the savannas is occurring concurrently with deforestation in the adjacent tropical forest biomes, so any climatic effect of savanna transformation would be reinforced by the effect of deforestation. In the Amazon, Nobre et al. (1991) predicted that climatic changes resulting from deforestation would cause the distribution of climate favorable to forest to recede by 500 to 1000 km in the southern Amazon, a region that would likely be replaced by tropical savanna. Similarly, where savanna grades into semiarid ecosystems, a similar retreat of savanna may be expected.

Understanding the strength of vegetation–climate feedbacks in tropical savanna will require more detailed knowledge in several areas. There is a paucity of information on the effect of tree density and aggregation on albedo and roughness length in such systems. Also required is greater knowledge of how precipitation amount and variability affect tree density both directly and indirectly through changes in fire frequency. Such information is important for understanding the climatic consequences of humans in tropical savannas.

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REFERENCES


