TREE LAYER SPATIAL STRUCTURE CAN AFFECT SAVANNA PRODUCTION AND WATER BUDGET: RESULTS OF A 3-D MODEL

GUILLAUME SIMIONI, JACQUES GIGNOUX, AND XAVIER LE ROUX

1Laboratoire Fonctionnement et Evolution des Systemes Ecologiques, Universite Paris 6-CNRS-ENS, 46 rue d’Ulm, 75230 Paris cedex 05, France
2U.M.R. PIAF (INRA-Universit´e Blaise Pascal), Site de Crouelle, 234 avenue du Br´ezet, 63039 Clermont-Ferrand cedex 02, France

Abstract. The spatially explicit and mechanistic model TREEGRASS was used to test the effects of tree density, tree spatial distribution, and tree size distribution on radiation absorption, net primary production (NPP), and water fluxes for a West African savanna. The model has previously been shown to adequately predict radiation absorption, production, and soil water balance in humid savannas. Using field measurements quantifying the spatial variations in grass NPP, the model was found to predict correctly the effect of tree abundance on NPP. Model simulations showed that annual photosynthetically active radiation (PAR), absorption efficiency, NPP, and transpiration of the tree layer increased with increasing tree density and decreased with increasing tree aggregation; the grass layer showed the opposite trends. Total NPP (tree plus grass) remained stable for all tree densities and decreased slightly for aggregated tree distributions. Total transpiration increased with tree density and was not affected by tree aggregation. Changing the tree size distribution had no effect on radiation absorption or on carbon and water fluxes.

This study showed that fine-scale vegetation structure can influence NPP and water fluxes. As such, it should be taken into account when assessing the functioning of tree-grass systems. However, the detailed fine-scale structure of the tree layer is rarely available for savanna ecosystems. Thus we assessed the reliability of two common descriptors of savanna vegetation, leaf area index (LAI) and tree canopy cover, to predict PAR absorption, NPP, and evapotranspiration. Neither of these descriptors could adequately predict all the simulated effects. However, tree canopy cover can be used to reasonably estimate radiation absorption and carbon fluxes, whereas LAI is a good predictor of water fluxes. Therefore, mapping and monitoring approaches incorporating both LAI and tree canopy cover appear to be suitable alternatives to quantifying the fine-scale vegetation spatial structure when assessing ecosystem function in savanna-like ecosystems.

Key words: evaporation; Ivory Coast; Lamto; leaf area index (LAI); net primary production; spatial patterns; three-dimensional ecosystem models; three-dimensional ray tracing; transpiration; tree cover; tree-grass interactions.

INTRODUCTION

The necessity of assessing effects of global change on terrestrial ecosystems has spurred on the emergence of a new scientific field: ecosystem physiology. It aims at understanding and predicting energy and mass fluxes at the whole ecosystem level (Mooney et al. 1999) or even higher, up to the biosphere system (Candell et al. 2000). Specific techniques have been developed to address these issues, among which are ecosystem modeling at a global scale (Prentice et al. 1992, Melillo et al. 1993, Sellers et al. 1997), remote sensing (Tucker et al. 1986, Sellers et al. 1994), and whole ecosystem experiments (Baldocchi et al. 1997, Miranda et al. 1997, Hendrey et al. 1999). Whole ecosystem experiments provide estimates of carbon and water fluxes at the ecosystem scale that can be used to extrapolate fluxes at the regional or biome scales. But these measurements generally fail to detail underlying ecosystem processes that lead to ecosystem fluxes, unless they rely on complex methods like deconvolution analysis by inverse modeling (Luo et al. 2001). On the other hand, gas exchange measurements on ecosystem components like soil or leaves do not provide all the clues to scale up and predict fluxes measured at the whole ecosystem level. Indeed, scaling up from the leaf to the ecosystem and from the day to time spans relevant to climate change issues requires the knowledge of some processes not well understood. In particular, there is a need to better account for phenology (Lechowicz and Koike 1995, Canadell et al. 2000), biodiversity and demography (Pacala and Deutschman 1995, Moorcroft et al. 2001), and the spatial organization of plant individuals (Pacala and Deutschman 1995, Simioni et al. 2000).
The spatial organization of plant individuals is considered a prominent factor influencing plant ecology (Tilman and Kareiva 1997, Murrell et al. 2001). Many studies have reported its importance on plant demography (Barot et al. 1999), coexistence and competition (Chesson and Warner 1981, Bengtsson et al. 1994, Bolker and Pacala 1999), and population genetics (Antonovics and Levin 1980, Doligez et al. 1998). However, the importance of the spatial organization of plant individuals for ecosystem production and water balance has received much less attention. This may be due to the difficulty of coping simultaneously with detailed representations of ecosystem structure and plant eco-physiology, but also due to the fact that models ignoring spatial patterns of plant individuals did yield satisfying results for forest and grassland ecosystems, on which most studies have been conducted (Urban et al. 1991, Coughenour and Chen 1997, Leriche et al. 2001). In open systems such as savannas, fallows, recolonized old fields, and other transition systems, vegetation structure is conspicuously heterogeneous (Scholes and Archer 1997), but the role of vegetation structure on ecosystem functioning is not well understood. Yet there is a growing recognition of the importance of understanding savanna functioning. Tree-grass systems cover a large fraction of terrestrial surfaces (Solbrig et al. 1990, Scholes and Hall 1996), but we lack comprehensive data sets to predict carbon fluxes at the savanna biome level (Canadell et al. 2000; House et al., in press).

The aims of this research were (1) to test whether the spatial structure of the tree layer can have significant effects on carbon and water fluxes in savanna ecosystems, and then (2) to propose bulk parameters for taking into account the effects of vegetation organization on ecosystem fluxes in coarse resolution models. We used the three-dimensional model TREEGRASS (Simioni et al. 2000) to assess the effects of the fine-scale spatial structure of the tree layer on net primary production (NPP) and water balance for small savanna areas (from 100 to 10,000 m²) over one vegetation cycle. We present the main features of TREEGRASS, parameterized for the savanna of Lamto (Ivory Coast) and already tested against field data (Simioni et al. 2000). The ability of the model to correctly predict the effect of tree abundance on grass NPP was tested here using field measurements quantifying the spatial variations in grass NPP. Using simulation experiments, the effects of tree density, tree spatial distribution, and tree crown size distribution on NPP and water fluxes were tested at the ecosystem scale (annual NPP and evapotranspiration of the combined tree and grass components) and at the scale of the tree and grass components (annual total tree NPP and transpiration vs. annual total grass NPP and transpiration). Simulation outputs were reused in order to test the ability of two common vegetation descriptors, leaf area index (LAI) and tree canopy cover, to predict NPP and water losses of tree, grass, and grass plus tree components at the ecosystem scale. Implications for vegetation monitoring and the representation of vegetation in models of mixed tree–grass ecosystems at larger scales are discussed.

METHODS

The TREEGRASS model

TREEGRASS is a spatially explicit, individual plant-based model that simulates water fluxes and net primary production (NPP) for small tree–grass areas (tree plus grass layers; 100–10,000 m²) over one to a few vegetation cycles, with a daily time step. Competition for light and water is treated mechanistically (i.e., most relationships used are biophysical). It includes sub-models derived from the three-dimensional RATP model (Radiation Absorption, Transpiration, and Photosynthesis; Sinoquet et al. 2001) that computes radiation and energy budgets within vegetation canopies, and from the PEPSEE model (Production Efficiency and Phenology in Savanna Ecosystems; Leriche et al. 2001) that simulates primary production and soil water balance in savanna grasslands. It works within the MUSE simulation framework (Multi-strata Spatially Explicit model; Gignoux et al. 1996) that provides background algorithms for spatially explicit ecosystem modeling. A full description of TREEGRASS is presented in Simioni et al. (2000). The main features of TREEGRASS follow here:

1) Space is divided into a three-dimensional grid of cells (Fig. 1). Cell size can be defined to fit with the sizes of vegetation components. Aboveground cells can contain homogeneous grass, tree, or grass and tree foliage elements. There are three layers of belowground cells: layer 1, which includes 90% of grass roots; layer
2, which contains all remaining grass roots; and layer 3, the deep soil underneath.

2) The grass layer is divided into plots or pixels corresponding to grid cell basal dimensions. Each grass plant is relegated to its own pixel; its foliage occupies one aboveground cell and its roots are distributed in the two soil cells underneath. Each individual tree canopy is assumed to occupy a cylindrical volume, referred to as a foliage crown. Similarly, each individual tree root system is assumed to occupy a root crown. Tree height, bole height (bottom of canopy), foliage and root crown radii, and peak leaf area index of individual trees are linked by allometric relations. Tree leaves and roots are located in aboveground and belowground cells, according to overlap coefficients between crown cylinders and grid cells (Fig. 1). Stems and branches are not explicitly represented. Two grass "individuals" (i.e., grass pixels) do not overlap. By contrast, tree crowns can overlap grass cells and other tree crowns. In the following, any cell containing leaves will be named "vegetation cell," and the different types of leaves sharing one vegetation cell will be referred to as "entities." Coarse and fine roots are not differentiated. Given that only simulations over short periods (typically 1 yr) are made, tree dimensions are assumed to be fixed, only leaf area density and root mass density can change within individual foliage and root crowns.

3) A radiation absorption submodel, derived from Sinoquet et al. (2001), calculates the amounts of photosynthetically active radiation (PAR), near infrared radiation, and thermic infrared radiation absorbed or emitted at each time step by each entity in each vegetation cell, and by the soil surface. This submodel accounts for daily and yearly solar heights and azimuths, diffuse radiation, and reflection-transmission by foliage entities and soil. Radiation balance depends on leaf area density and leaf angle distributions in each vegetation cell, and species-specific leaf optical properties. Radiation absorption is computed five times a day, to account for diurnal variations in radiation absorption, air vapor pressure deficit, and air temperature.

5) Amounts of transpired water for each entity in each vegetation cell are summed to yield individual plant transpiration rates. Plant water uptake depends on root spatial location, but not on root biomass or density (assuming that active and nonactive roots have identical spatial locations). Thus soil moisture may not be identical in all soil cells from a same layer. Under nonlimiting water conditions, water transpired by a given individual plant is extracted in layers 1 and 2 in cells where its roots are present. More water is extracted from layer 2 as water stress becomes more pronounced. The water stress experienced by each plant depends on the soil water content in layer 1, in cells where its roots are present.

6) When rainfall occurs, runoff is computed according to the degree of soil coverage by vegetation and rainfall amount. The remaining water is an input that increases soil water content in layer 1. Drainage occurs from layer 1 to layer 2, and into layer 3, when soil water content in a given layer exceeds field capacity.

7) Total absorbed PAR by each plant is converted into dry matter using the light use efficiency (LUE) approach (Monteith 1972, 1977). The actual LUE is computed according to a species-dependent, maximum LUE constrained by water stress.

8) The ratio of the dry matter production allocated to roots vs. shoots is computed as a function of the ratio of the actual to maximum LUE (Landsberg and Waring 1997) and thus depends on water stress. As water stress increases, the proportion of dry matter allocated to roots increases.

9) Grass leaf mortality is a function of grass physiology. The decomposition rate of dead leaves is assumed to be constant. Tree leaf mortality depends on tree phenology and water stress.

Parameterization for the Lamto savanna

The vegetation structure of the Lamto Natural Reserve (5°02' W; 6°13' N) has been described by Menaut and César (1979). Interannual rainfall variability is important with annual rainfall ranging from 800 to 1600 mm, with a mean of 1200 mm. Mean annual temperature is stable at ~27°C. The reserve presents a mosaic of forest along streams, and of savanna areas. Savanna areas present a high variability in the structure of the tree layer, from savanna grasslands to dense shrublands. Altitudes range from 75 to 125 m. The topography is very smooth with a mean ground slope of ~5%. Soil is composed of 75–80% sand and 7.5–15% clay.
clay; it is classified as ferralsol (according to the FAO classification). Soil depth ranges from 1 to 2 m.

Daily radiation, rainfall, wind speed, and daily courses of air temperature and air humidity measured at Lamto were used as input variables and assumed to be spatially homogeneous on the site. The grass considered here was the C₄ perennial bunch grass Hyparrhenia spp. (Andropogonaceae). The tree type represented in the model was Crossopteryx febrifuga, a dominant, deciduous, shallow-rooted species. In this tree species, 70% of the roots are located in soil layer 1 and remaining roots in soil layer 2. Tree root crown radius is 1.5 times the foliage crown radius (Mordelet 1993). Important parameters in the context of this study are summarized in Table 1. A full description of the parameters used for the study site and tests against field data on radiation absorption, production, and soil water balance in open and shrubby areas can be found in Simioni et al. (2000).

### Ability of TREEGRASS to predict the effect of tree cover on grass standing mass

In addition to already published model tests, a spatial test was performed to assess the ability of TREEGRASS to reproduce the effect of tree cover on grass production. Hemispherical photographs were taken skywards above 1 × 1 m grass plots at Lamto from 16 October to 26 October 2000, with a Canon AL-1 camera equipped with a Canon 7.5 mm fish-eye lens. Photographs were taken for 15 grass plots without nearby trees, 8 plots under tree clumps, and 10 plots at different distances (0–5 m) from a tree. In the same plots, grass aboveground parts were collected from 8 December 2000 to 4 January 2001, dried 1 wk at 70°C, and weighed. For each hemispherical photograph, sky openness (fraction of sky above the grass layer that was not obstructed by tree foliage elements) was computed using the GLA software (Gap Light Analyzer; Fraser et al. 1999). The regression between grass aboveground phytomass and sky openness was highly significant ($R^2 = 0.82$, $P = 0.0001$).

In order to test the ability of TREEGRASS to reproduce this grass production–sky openness relationship, a simulation was done with a shrubby savanna site of 14 × 14 m with 20 randomly located and even sized trees (see the corresponding map in Fig. 2). Such a site presents a large range of light conditions for grass pixels. Climate data from the year 2000 were used (at Lamto, a vegetation cycle is 1 yr from January to January, at dates when fire is set). Given the higher fertility of this site compared to the site studied by Le Roux (1995), a higher grass maximum conversion efficiency (4 g dry matter/MJ absorbed PAR; Simioni 2001) was used. For each simulated 1 × 1 m grass pixel, means of sky openness and grass aboveground phytomass were calculated for the dates corresponding to field measurements, to allow comparison of simulated with observed sky openness and grass phytomass.

### Simulation experiments

All experimental simulations were done using representative plots of 196 m² (14 × 14 m). Plots were divided into grids of 1 × 1 m cells, thus involving 196 grass pixels. The accuracy of the 1 × 1 m resolution

---

**Table 1. Main parameters used in the TREEGRASS model for simulations of the Lamtosavannas.**

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Values</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Photosynthetically active radiation absorbance (fraction of incoming PAR)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground</td>
<td>0.76</td>
<td>Le Roux et al. (1997)</td>
</tr>
<tr>
<td>Grass, green leaves</td>
<td>0.78</td>
<td>Le Roux et al. (1997)</td>
</tr>
<tr>
<td>Grass, dead leaves</td>
<td>0.35</td>
<td>Le Roux et al. (1997)</td>
</tr>
<tr>
<td>Tree, green leaves</td>
<td>0.78</td>
<td>NA†</td>
</tr>
<tr>
<td>Near infrared radiation absorbance (fraction of incoming NIR)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground</td>
<td>0.50</td>
<td>Le Roux et al. (1997)</td>
</tr>
<tr>
<td>Grass, green leaves</td>
<td>0.04</td>
<td>Le Roux et al. (1997)</td>
</tr>
<tr>
<td>Grass, dead leaves</td>
<td>0.05</td>
<td>Le Roux et al. (1997)</td>
</tr>
<tr>
<td>Tree, green leaves</td>
<td>0.10</td>
<td>NA†</td>
</tr>
<tr>
<td>Maximum stomatal conductances (mmol·m⁻²·s⁻¹)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>230</td>
<td>Seuer (1995)</td>
</tr>
<tr>
<td>Tree</td>
<td>230</td>
<td>NA†</td>
</tr>
<tr>
<td>Maximum conversion efficiencies (g dry matter/MJ absorbed PAR)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>2.28</td>
<td>Le Roux et al. (1997)</td>
</tr>
<tr>
<td>Tree</td>
<td>1.60</td>
<td>A. Bégut, personal communciation</td>
</tr>
<tr>
<td>Fraction of roots in soil layer 1 (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>90</td>
<td>Le Roux (1995)</td>
</tr>
<tr>
<td>Tree</td>
<td>70</td>
<td>Le Roux et al. (1995)</td>
</tr>
</tbody>
</table>

† NA = reference not available.
‡ Reference not available when simulations were performed, but supported by recent field measurements (Simioni 2001).
Tree density experiment

N = 2

Tree spatial distribution experiment

N = 20

HR  LR  R  LA

N = 20

HA  L  S

N = 40

HR  R  LA  HA

Tree size distribution experiment

N = 20

U  2  N  LN

map

profile

FIG. 2. Maps of the 14 x 14 m sites used for the simulations with the TREEGRASS model. Tree canopies and trunks are represented by circles and dots on the maps, and by squares and sticks in the profile views; N = number of trees per plot. Grass individuals are not shown. For tree spatial distribution, abbreviations are: HR, highly regular; LR, loosely regular; R, random; LA, loosely aggregated; HA, highly aggregated; L, in line; S, in square. For tree size distribution, abbreviations are: U, unique size; 2, two sizes; N, normal; LN, lognormal. Trees in density and size distribution experiments were randomly distributed, and a unique density (20 trees) was used for the tree size distribution experiment. Individual tree size was unique for tree density and spatial distribution experiments.

has been discussed in Simioni et al. (2000). The spatial structure of the tree layer on a plot is a combination of three components: tree density, spatial distribution, and crown size distribution. One set of simulations was performed for each of these components (Fig. 2). Each set was associated with the variation of only one parameter.

1) The effects of tree density were explored using a tree number on the whole plot ranging from 0 to 80 trees (i.e., from 0 to 4082 trees/ha). For each density, a random tree spatial distribution was generated using a Poisson process. For all these simulations, a unique tree size was used (height = 3.61 m; canopy area = 4 m²).

2) Seven tree spatial distributions were tested, ranging from regular to highly aggregated, in each of 2 densities (20 and 40 trees/plot). Regular distributions were generated using a sequential inhibition process (Gignoux et al. 1999), with an inhibition distance of 1.5 m (highly regular) or 0.5 m (loosely regular). Random distributions were generated as in (1). Aggregated distributions were generated by a Poisson cluster process (Gignoux et al. 1999): parent points were generated, to which child points were associated. Child points were distributed with a normal distribution centered on parent point positions, using a mean tree number per clump of 8 and 2.5 for loosely and highly aggregated distributions, respectively, and a mean clump radius of 2.8 m and 0.7 m for loosely and highly aggregated, respectively. The "line" and the "square" distributions were obtained by a random distribution within a 1 m wide line, and within a 4 x 4 m square. For all these simulations, a unique tree size was used as in (1).

3) The effects of the tree size distribution were tested using 4 size class distributions: a unique tree size (3.61 m high), 2 size classes (trees split between 2 height classes: 2 m and 4.82 m), a normal size distribution (tree heights ranging from 1.91 m to 5.57 m), and a lognormal size distribution (tree heights ranging from 0.2 m to 14.85 m). For all these simulations, tree density (20 trees) and maximum leaf area index (LAI) of the whole tree layer were constant, and tree spatial distribution was random as in (1).

For all experimental simulations, the model was run for one annual vegetation cycle (climatic data from
January 1991 to January 1992) that starts and ends at dates when fire occurs. This vegetation cycle presents a typical annual rainfall, and corresponds to field measurements used to test TREEGRASS in Simioni et al. (2000). Climate conditions were thus identical for all experimental simulations. To quantify the effects of tree spatial structure on ecosystem function, model outputs included absorbed PAR, aboveground and belowground NPP, transpiration and soil evaporation, and mean green LAI for the tree, grass, and the pooled tree plus grass component over the year.

Ability of LAI and tree canopy cover to describe NPP and water balance

In our simulations, when expressed at the total system scale, green LAI can be considered as a nonspatial parameter, as a given LAI value can correspond to various tree spatial distributions. By contrast, tree canopy cover (the ratio of projected crown surface to total plot area) implicitly includes spatial information because it depends on both tree density and tree spatial distribution (at a given tree density, tree cover decreases when overlap between tree crowns increases). Results of the simulations were reinterpreted in terms of annual averaged green LAI and tree cover. A regression analysis was done to assess the ability of LAI and tree canopy cover to predict grass, tree, or grass plus tree PAR absorption efficiency, NPP, and transpiration. Best regression fits were searched for pooled data sets, including all simulation types. Regression coefficient values were used to compare LAI and tree cover reliability.

RESULTS

Simulated effects of tree cover on grass production

The model was able to reproduce the effect of tree cover on grass production regardless of the spatial position of grass pixels (Fig. 3). An analysis of covariance was carried out to assess any difference between simulated and observed correlation between grass phytomass and sky openness. Intercepts and slopes were not significantly different between observed and simulated grass production ($P > 0.1$).

Effects of tree spatial structure

Effects of tree density.—Total photosynthetically active radiation (PAR) absorption efficiency (tree plus grass components over the whole plot) increased by 54% when tree density increased from 0 to 80 trees/plot (Fig. 4). The increase in PAR absorption efficiency of trees thus overcompensated for the decrease in grass PAR absorption efficiency. Total net primary production (NPP) remained roughly constant with increasing tree density, because the increase in tree NPP proportionately compensated the decrease in grass NPP (Fig. 4). Annual total evapotranspiration increased by 360 mm with increasing tree density. When tree density increased from 0 to 80 trees/plot, annual grass transpiration was reduced by 390 mm, while annual tree transpiration increased by 770 mm. Soil evaporation decreased slightly with increasing tree density (Fig. 4). The decreases in grass PAR absorption efficiency, grass NPP, and grass transpiration with increasing tree density were all highly nonlinear. Grass, tree, and total water use efficiencies (WUE, ratio of production to transpiration) decreased with increasing tree density. No effect of tree density was found on the partitioning of tree, grass, and tree plus grass NPP between aboveground and belowground parts. The overall aboveground to belowground NPP ratio was 1.45.

Effectsof treespatial distribution.—For aggregated distributions, grass PAR absorption efficiency was higher and tree PAR absorption efficiency lower than for random or regular distributions (Fig. 5). These two trends did not fully compensate, and total PAR absorption efficiency by the tree plus grass vegetation decreased with increasing tree aggregation at both tree densities (-14% for 20 trees/plot, -10% for 40 trees/plot). Total NPP only slightly decreased with increasing tree aggregation (-7% for 20 trees/plot, -9% for 40 trees/plot); the increase in grass NPP largely compensating for the decrease in tree NPP (Fig. 5). With increasing tree aggregation, soil evaporation and total evapotranspiration remained constant, with increases in grass transpiration being fully compensated for by declines in tree transpiration. When tree aggregation increased, grass WUE increased slightly while that of trees decreased. Whole system WUE slightly decreased (results not shown). Qualitatively, similar results were obtained for the two tree densities studied.
changing the tree spatial distribution only slightly influenced the response of total NPP to changes in tree density (Fig. 6). But it significantly affected the shape of the nonlinear decrease in grass NPP with increasing tree density. Grass NPP decreased more importantly with highly regular tree distributions and less importantly with aggregated tree distributions.

Effects of tree size distribution.—PAR absorption efficiency, NPP, and transpiration rates of grasses and trees were insensitive to tree size distribution (results not shown). Tree transpiration exhibited the highest change with changing tree size distribution (+9% from uniform to lognormal distributions).

Leaf area index (LAI) and tree cover as predictors of the functioning of the grass, tree, and grass plus tree components

Annual PAR absorption efficiency, NPP, and transpiration of the grass layer were strongly correlated to grass green LAI and to tree canopy cover (Fig. 7). Unique relationships were obtained for the range of tree densities, spatial distributions, or crown size distributions examined. For the tree layer, PAR absorption efficiency and NPP were strongly correlated to tree cover (Fig. 8). By contrast, the relationship between tree PAR absorption efficiency and LAI, or NPP and tree LAI, was sensitive to the type of tree spatial distribution. At 20 trees/plot, from highly regular to highly aggregated tree distributions, tree NPP decreased by 43% while tree LAI was constant. Annual tree transpiration was highly correlated to tree LAI, while a weaker relationship was obtained when tree cover was used as the independent variable (Fig. 8). Annual PAR absorption efficiency by the tree plus grass layers was well correlated with tree cover, but much less with total green LAI (Fig. 9). Total NPP changed little but was significantly correlated with tree cover, but not with total green LAI. Soil evaporation, total transpiration, and total evapotranspiration were highly correlated with total green LAI when data were pooled across all tree spatial or crown size distributions. By contrast, the correlation between total transpiration or total evapotranspiration and tree cover was sensitive to the type of tree spatial distribution.

Discussion

Model tests

The ability of TREEGRASS to reproduce grass biomass and necromass dynamics for a pure grass stand, soil water content out and under a tree clump, and photosynthetically active radiation (PAR) absorption by the tree layer for a tree-grass plot has previously been tested (Simioni et al. 2000). The test, results of which are presented in this paper, was carried out to assess the ability of the model to reproduce the intrasystem spatial heterogeneity of grass production. Such a high spatial heterogeneity has already been observed in several savanna ecosystems (e.g., Scanlan and Burrows 1990). Test results strongly support the ability of TREEGRASS to reproduce tree-grass interactions. To our knowledge, it is the first time that a spatially explicit model has been tested against mea-
Effects of tree spatial structure on grass, tree, and total net primary production (NPP) and transpiration.

**Effects of the tree spatial structure on NPP.**—In the last decade, two controversial questions regarding the influence of the tree layer structure (especially tree density) on the function of tree–grass systems have been raised. (1) How does grass and tree NPP change with changes in the structure of the tree layer? And (2) what is the influence of the structure of the tree layer on total (tree plus grass) ecosystem production?

In many savannas, grass production declines when tree density increases (reviewed by Scholes and Hall 1996). The observed shape of the grass NPP response curve with changes in tree density can be concave (Walker et al. 1972, Beale 1973), linear (Walker et al. 1986), or convex (Aucamp et al. 1983). These differences in shape are commonly attributed to differences in the potential site productivity (referred to as the potential grass production without trees) that depends on site fertility and rainfall (Scanlan and Burrows 1990) or to disturbance (e.g., grazing) regimes (McPherson 1992). In our simulations, for a given (i.e., random) tree distribution, changes in tree and grass NPP with increasing tree density were nonlinear. The decrease in grass NPP with increasing tree density was influenced by the tree spatial distribution (Fig. 6). Soil fertility and rainfall were identical in all simulations, suggesting that, for a given site productivity, the relationship between grass NPP and tree density can vary in response to the spatial structure of the tree layer. In this humid savanna, this nonlinearity is probably due to competition between trees for PAR. Trees have first access to light, but when tree density or aggregation increases, tree–tree competition for PAR increases as distances between trees decrease. Then, an individual tree absorbs less PAR, on average (as can be inferred from the data).
The occurrence of NPP stability with increasing tree abundance depends on the savanna system being considered.

**Effects of tree spatial structure on water fluxes.**—Predicting the effects of vegetation cover on water fluxes at the soil-plant-atmosphere interface is important from a hydrological or meteorological point of view. However, there is little information available on the effect of tree density on grass, tree, and total transpiration in savannas. Our results are in accordance with experiments of Eastham and Rose (1988) who found that grass transpiration decreased with increasing tree density, and of Eastham et al. (1990) in which total tree transpiration increased with increasing tree density. Our simulated increases in total evapotranspiration with increasing tree density are consistent with field measurements in tropical agroforestry systems and the arid dehesas of South Spain. These measurements showed that evapotranspiration of tree–grass stands was greater than that of pure grass stands by about 100% (Tournebize et al. 1996), and by 25–65% (depending on year and site; Joffre and Rambal 1993).

Overall, grass and tree transpiration changed less than grass and tree NPP when tree density or aggregation increased. In the energy balance calculation, transpiration depends on net absorbed radiation (i.e., PAR plus infrared radiation), but infrared radiation penetrates foliage better than PAR, and infrared absorption is thus less influenced by the vegetation structure. This led to a less spatially heterogeneous distribution of transpiration than production, reflected in the fact that water fluxes were better correlated to green leaf area index (LAI) (a nonspatial vegetation descriptor) than to tree cover. This explains the stability of total transpiration with tree spatial distribution and with tree size distribution, as total green LAI did not change with these.

**Consequences for tree–grass ecosystem functioning and for the mapping and monitoring of savannas.**—Tree encroachment has been observed in many savannas worldwide (Polley et al. 1997, Archer et al. 2001), including at Lamto over the last 30 yr (Gautier 1989, Dauguet and Menaut 1992). If changes in tree cover occur in Guinea savannas, our results show that a change in the water balance, with an increase in the evaporative fraction (i.e., annual evapotranspiration to rainfall ratio), can occur. Potential impacts of such a change on hydrology and climate need to be explored. A preliminary study coupling a simplified version of TREEGRASS with a hydrological model stressed the importance of taking into account the vegetation cover to predict water balance of a Sahelian savanna at the landscape scale (Boulain 2000).

If no major change in annual total NPP is expected in the case of tree encroachment, the contribution of trees to total NPP can increase. Part of tree NPP is
stored in woody organs that do not burn, or burn very little, when fire occurs; whereas all aboveground grass phytomass is released into the atmosphere with fire. Therefore, during a shift from grass-dominated to tree-dominated savannas, even if total system NPP is stable, less carbon would be released into the atmosphere. The study suggests that the magnitude of this effect depends on the tree spatial distribution, emphasizing the need to use adequate vegetation descriptors in field studies.

**Tree cover and LAI as predictors of savanna function.**—Results of the simulations show that if we focus only on total fluxes (water or NPP) at the system level, failure to consider the spatial structure of the vegetation will have little consequence. On the other hand, any study that needs to separate grass and tree functioning cannot ignore tree density and spatial distribution, as both strongly affect grass and tree PAR absorption efficiencies, NPP, and transpiration. Simply measuring...
LAI, for example, would not be sufficient to characterize function in mixed tree-grass systems, without documenting tree aggregation. Other studies have stressed the importance of spatial patterns in the functioning of forest ecosystems (e.g., Pacala and Deutschman 1995, Gastellu-Etchegorry and Trichon 1998). Our results suggest that combining tree cover and LAI would be appropriate for describing tree spatial structure and predicting its effects on carbon and water fluxes in savanna ecosystems.

**Limits of model predictions**

Spatial and temporal distribution of nutrient availability.—In various savannas (Belsky et al. 1989, Weltzin and Coughenour 1990, Vetaas 1992, Rhoades 1997) including Lamto (Mordelet et al. 1993), nutrient availability was found to be spatially heterogeneous, with nutrient-rich soils located under tree cover. Along with better water conditions, this higher nutrient availability explains grass NPP enhancement under tree cover observed in some savanna ecosystems (e.g., Weltzin
and Coughenour 1990, Belsky et al. 1993). Indeed, nutrients are known to greatly influence photosynthesis (Field and Mooney 1986), assimilate allocation (Wilson 1988, Ingestad and Agren 1991, Tan and Hogan 1998), and influence respiration (Ryan 1995). Cruz (1997) observed an increase of the light and nutrient use efficiencies of a C4 grass under tree cover. All the simulations made in the present study assumed a constant light use efficiency between grasses growing in open areas and under tree cover, but this did not affect the model accuracy to reproduce the effect of tree cover on grass production (Fig. 3).

Nutrients were not represented explicitly in this first version of TREEGRASS, for sake of simplicity. In the near future, we plan to include detailed physiological production processes (photosynthesis, respiration, carbon and nitrogen partitioning), and a soil organic matter decomposition model (the SOMKO model; Gignoux et al. 2001), to account for nitrogen processes.

Fig. 9. Variations in total PAR absorption efficiency, NPP, transpiration, and evaporation, with tree cover and total annual mean green LAI. See Fig. 7 for symbol definitions; abbreviations are: tr., transpiration; evap., soil evaporation; evapotr., evapotranspiration. No significant correlation was found between total NPP and total mean green LAI.
**Functional diversity of the grass and tree layers.**— Although the model TREEGRASS is able to represent plots with different plant species, only one grass species and one tree species were considered in the present study. This is a simplification of most real savanna ecosystems, because the specific composition of the grass layer can differ under tree cover and in open areas (Belsky et al. 1993, Scholes and Archer 1997). Furthermore, tree species that differ in their ability to acquire spatially heterogeneous resources co-occur in savannas (Montaña et al. 1995, Breshears et al. 1997, Le Roux and Bariac 1998, Jackson et al. 1999). In particular, two dominant tree species present at Lamto are known to have different water uptake behaviors (Konaté et al. 1998, Le Roux and Bariac 1998). Although beyond the scope of the present paper, the impact of the functional diversity (presence of different grass and/or tree species having distinct strategies of water uptake or growth) on the savanna functioning will have to be tested in future studies.

**Tree architecture.**—In this study, tree-tree competition did not influence tree architecture (i.e., trees, whether isolated or aggregated, had a cylindrical shape). But in forests or woodlands, tree crown shape can be influenced by the presence of neighbors (Sorrensen-Cothern et al. 1993, Moravie et al. 1997). Foilage crown shape can influence the acquisition of light resources (Kuuluvainen and Pukkala 1989, Vales et al. 1993, Moravie et al. 1997) whereas species-specific plasticity of crown growth patterns sometimes partly determines the competitive ability of co-occurring tree species (Williams 1996). A similar phenomenon is expected belowground (Eastham and Rose 1990), and can be important in predicting competition for water and nutrients. Thus, including tree shape plasticity in TREEGRASS could improve its predictive capacity.

**Climatic variables.**—In the field, climatic variables are not always spatially homogeneous: temperature, vapor pressure deficit, and wind vary vertically and horizontally both at plot scale and within plant foliage (Tuzet et al. 1997, Daudet et al. 1999). However, explicit computations of feedbacks between plant function and air characteristics would be hardly integrated in an ecosystem model like TREEGRASS, because of computing time limitations. Moreover, the spatial distribution of microclimatic variables is not always of prime importance in determining the distribution of plant functioning. For instance, the spatial distribution of wind was found to have a negligible effect on transpiration and photosynthesis within an individual tree crown (Daudet et al. 1999).

**CONCLUSION**

Total evapotranspiration was sensitive and total NPP was insensitive to the spatial structure of the tree layer. However, the balance between grass and tree functioning was sensitive to both tree density and spatial distribution, but not tree size distribution. Because these effects can be of prime importance for the whole system dynamics, further studies are needed to test interactions between carbon and water fluxes and three-dimensional ecosystem structure and dynamics at larger time and/or spatial scales.

**ACKNOWLEDGMENTS**

We thank two anonymous reviewers for helpful comments on an earlier version of the manuscript. This work was supported by the “Programme National de Recherche en Hydrologie” (PNRH), and by the “European Terrestrial Ecosystem Modelling Activity” (ETEMA).

**LITERATURE CITED**


Fraser, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyser (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs: user’s manual and program documentation. Simon Fraser University, Burnaby, British Columbia, Canada, and the Institute of Ecosystem studies, Millbrook, New York, USA.


characteristics. Agricultural and Forest Meteorology 43: 201–223.


