

A biogeochemistry-based dynamic vegetation model and its application along a moisture gradient in the continental United States

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Abstract. We develop and evaluate a large-scale dynamic vegetation model, TEM-LPJ, which considers interactions among water, light and nitrogen in simulating ecosystem function and structure. We parameterized the model for three plant functional types (PFTs): a temperate deciduous forest, a temperate coniferous forest, and a temperate C₃ grassland. Model parameters were determined using data from forest stands at the Harvard Forest in Massachusetts. Applications of the model reasonably simulated stand development over 120 yr for *Populus tremuloides* in Wisconsin and for *Pinus elliottii* in Florida. Our evaluation of tree-grass interactions simulated by the model indicated that competition for light led to dominance by the deciduous forest PFT in moist regions of eastern United States and that water competition led to dominance by the grass PFT in dry regions of the central United States. Along a moisture transect at 41.5° N in the eastern United States, simulations by TEM-LPJ reproduced the composition of potential temperate deciduous forest, temperate savanna, and C₃ grassland located along the transect.

Keywords: Biogeochemistry; Biogeography; Plant functional type; TEM-LPJ; VEMAP.

Abbreviations: DGVM = Dynamic global vegetation models; LPJ = Lund-Potsdam-Jena; TEM = Terrestrial Ecosystem Model; VEMAP = Vegetation Ecosystem Modeling and Analysis Project; WBM = Water Balance Model.

Introduction

At large scales, biogeochemistry models have traditionally been used to assess responses of ecosystem function to projected changes in climate and atmospheric CO₂, while biogeography models have been used to simulate the response of biome boundaries to projected changes in climate and atmospheric CO₂ (Anon. 1995; Pan et al. 1998). The first phase of the Vegetation Ecosystem Modeling and Analysis Project (VEMAP) coupled large-scale biogeochemistry and biogeography

models in an asynchronous fashion and partitioned equilibrium responses of ecosystem net primary production (NPP) and carbon storage into functional and structural components (Anon. 1995). This experiment clearly indicated that responses of both ecosystem function and structure contributed substantially to the simulated continental responses of NPP and C storage. Thus, aspects of both biogeochemistry and biogeography models need to be considered so that models simultaneously consider interactions between function and structure. A new generation of global ecological models, known as dynamic global vegetation models (DGVMs), that simultaneously consider interactions between structure and function have recently emerged for studying the potential large-scale responses of terrestrial ecosystems to environmental change (Foley et al. 1996; Friend et al. 1997; Cramer et al. 1999, 2001; Daly et al. 2000).

A recent comparison of the responses of extant DGVMs to projected climate change, the DGVM inter-comparison, revealed substantial differences in both functional and structural dynamics among the models (Cramer et al. 1999, 2001). As the extant DGVMs are works in progress, and have not been extensively tested, it is not surprising that the models demonstrated substantially different responses to projected climate change. Most of the models emphasized how the availability of water and light influence ecosystem structure and C dynamics, and did not consider the role of nutrients, such as N or P, in influencing the function and structure of ecosystems. A number of studies suggest that nitrogen dynamics are likely to play a role in the responses of ecosystem function to climate change, particularly for ecosystems that occur at higher latitudes (Anon. 1995; McGuire et al. 1995a, 1997, 2000a, 2001; Clein et al. 2001). As anthropogenic N deposition may be contributing substantially to present-day C storage in the terrestrial biosphere (Schimel 1995; Townsend et al. 1996; Holland et al. 1997; Nadelhoffer et al. 1999; Lloyd 1999), it is

important to consider the role of N in modeling future responses of terrestrial ecosystems.

In this study we present the development and evaluation of a large-scale dynamic vegetation model, TEM-LPJ, that considers the effects of N dynamics on ecosystem function and structure. Biogeochemical processes in the model are derived from the Terrestrial Ecosystem Model (TEM), in which N exerts control over the rates of several C cycling processes (McGuire et al. 1997; Pan et al. 1998). Vegetation dynamics are derived from the Lund-Potsdam-Jena (LPJ) DGVM (Sitch 2000), which participated in the DGVM inter-comparison described in Cramer et al. (2001) and does not explicitly consider interactions between C and N dynamics. The C dynamics of both TEM and LPJ have been evaluated at seasonal, inter-annual, and longer-term time scales (Heimann et al. 1998; McGuire et al. 2000a, b, 2001).

Model description

Overview

TEM-LPJ is a biogeochemistry-based dynamic vegetation model that simulates ecosystem C, N and water interactions in the context of vegetation compositional changes of various plant functional types (PFTs) during stand development or recovery from a disturbance. Some of the features of TEM-LPJ are similar to the original TEM and LPJ models, but other features are different or new (Table 1). The interactions between biogeochemistry and vegetation processes in TEM-LPJ indicate how information is exchanged among different components of the model (Fig. 1). In contrast to some dynamic vegetation models which pass information annually between biogeochemistry and biogeography components (e.g. MC1; see Daly et al. 2000), interactions between the biogeochemical and vegetation dynamics components of TEM-LPJ occur at a monthly time step so that interactions for water, light, and N are considered simultaneously (Table 2).

The biogeochemistry component of the model simulates the monthly fluxes and pools of C and N for each PFT. Simulated NPP is allocated to reproductive effort and pools for different vegetation parts. The algorithm for allocation of NPP depends, in part, on competition for water and light (Table 1, Fig. 1). Biogeochemical processes including photosynthesis, NPP, litter-fall, and N uptake are modeled for each PFT based primarily on algorithms derived from TEM, but these processes are also influenced by changes in stand age and the relative abundance of PFTs as simulated by the vegetation dynamics component of TEM-LPJ. Water dynamics in TEM-LPJ is modeled by a modified version of water

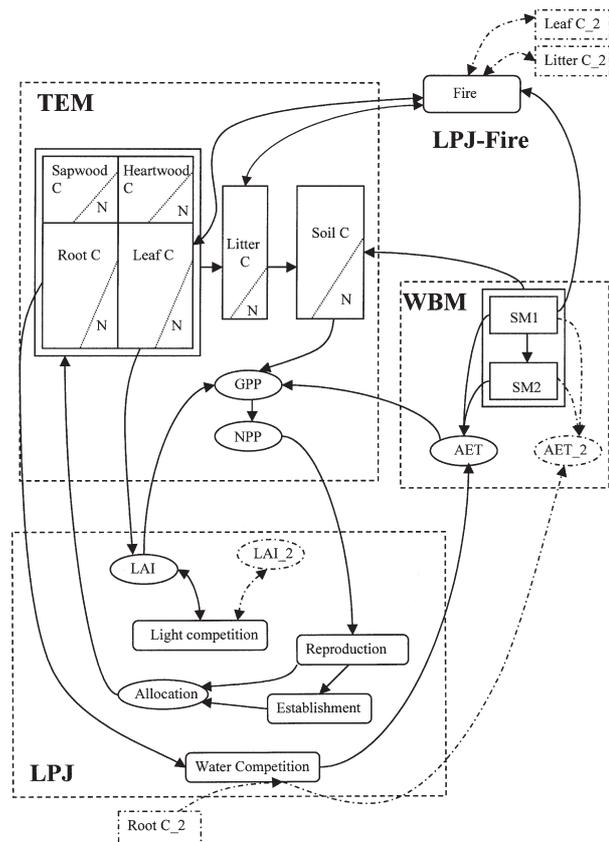


Fig. 1. Schematic of the TEM-LPJ model depicting the flow of information among a modified version of the Terrestrial Ecosystem Model (TEM), a modified version of the Water Balance Model (WBM) and algorithms from the Lund-Potsdam-Jena model (LPJ). Biogeochemical pools and fluxes are simulated by TEM, hydrology variables by WBM and vegetation dynamics including fire disturbances by modules from LPJ. Vegetation in the TEM component is now represented by four carbon/nitrogen pools: Sapwood, Heartwood, Root and Leaf. Hydrology in the WBM component is now represented by two soil moisture pools (SM1 and SM2). The influence of a second plant functional type on ecosystem structural and functional dynamics is represented by Leaf C₂, Litter C₂, AET₂, LAI₂ and Root C₂. GPP is gross primary production; NPP is net primary production; AET is actual evapotranspiration; and LAI is Leaf area index.

balance model (WBM; Vorosmarty et al. 1989), in which the soil profile has been divided into two layers based on rooting depths of different PFTs that compete for water resources in the two layers (Fig. 1).

The vegetation dynamics component of TEM-LPJ includes modules for reproduction, establishment and competition for light and water, and fire disturbance. The algorithms in these modules allow TEM-LPJ to model interactions among tree and grass PFTs that influence the composition of trees and grass in ecosystems. The fire disturbance modules simulate fire frequency and the effects of fire disturbance. Fire frequency is determined

Table 1. Comparison of model characteristics among TEM, LPJ and the coupled TEM-LPJ model.

Features	TEM	LPJ	TEM-LPJ
Vegetation carbon	One pool for a each plant functional type (PFT)	Four pools (leaf, root, sapwood, heartwood) for tree PFTs and two pools (leaf and root) for grass PFTs	Four pools (leaf, root, sapwood, heartwood) for tree PFTs and two pools (leaf and root) for grass PFTs
Soil carbon	One pool	Two pools	One pool
Vegetation nitrogen	Two pools (structural and labile pools)	Not represented	Two pools (structural and labile pools)
Soil nitrogen	Two pools (soil organic N and available N)	Not represented	Two pools (soil organic N and available N)
Litter	Included in soil carbon pool	One pool	One pool
Gross primary production and respiration	TEM equations	LPJ equations	TEM equations
Soil N mineralization	TEM equations	Not represented	TEM equations
N uptake	TEM equations	Not represented	TEM equations
Foliage effect on growth	Foliage seasonality	Foliage area	Foliage area and seasonality
Soil profile	One layer	Two layers	Two layers
Rooting depth	PFT-specific, depends on soil texture	Constant values for grasses (50 cm) and trees (100 cm)	PFT-specific, depends on soil texture
Water competition	Not represented	Competition related to rooting depth	Competition related to rooting depth, root biomass and water absorption efficiency
Light competition	Not represented	Competition related to foliage projected cover	Competition related to foliage projected cover
Nitrogen competition	Not represented	Not represented	Implicit and relative to carbon status
Reproduction	Not represented	LPJ reproduction module	LPJ reproduction module
Establishment	Not represented	LPJ establishment module	LPJ establishment module
Fire occurrence	Not represented	LPJ fire frequency model	LPJ fire frequency model
Fire disturbance	Not represented	LPJ fire disturbance module	LPJ fire disturbance module
PFT development	Mature	Successional	Successional

by the fuel-load, which varies by PFT, the number of dry days in a growing season, and the probability of fire ignition. The fire disturbance module also describes the burnt fractions of vegetation and soil C and affects biogeochemistry by modifying the C and N pools in the model.

Biogeochemistry

The TEM is a biogeochemistry model that uses spatially referenced information on climate, elevation, soils, and vegetation to estimate important C and N fluxes and pool sizes at a monthly temporal resolution (McGuire et al. 1993; Melillo et al. 1993; Fig. 2).

Version 4.1 of TEM, which was developed for simulations at seasonal to century time scales (Xiao et al. 1998; Tian et al. 1998, 1999, 2000; Kicklighter et al. 1999; McGuire et al. 2000a, 2000b, 2001; Clein et al. 2000, 2001), was used as the starting point for developing the biogeochemistry represented in TEM-LPJ.

For TEM-LPJ, we modified the gross primary production equation in TEM 4.1 so that changes in leaf biomass influence photosynthesis. This modification allows TEM-LPJ to simulate the age-dependent pattern of monthly carbon and nutrient dynamics for the forest, grassland, and savanna ecosystems considered in this study. Other modifications to TEM include dividing the single vegetation C pool into foliage, roots, sapwood and

Table 2. Interactions and feedbacks among biogeochemistry, vegetation dynamics, and fire modules/processes in TEM-LPJ.

Source from:	Target to:		
	Biogeochemistry	Vegetation dynamics	Fire
Biogeochemistry		Tree and grass leaf carbon (affecting light competition) Tree and grass root carbon (affecting water competition) Tree and grass NPP (for reproduction) Soil carbon and nutrient pools (affecting succession)	Tree and grass litter Carbon (fuel) Grass leaf carbon (fuel) Upper layer soil moisture (fuel moisture)
Vegetation	Consumption of NPP in reproduction (dynamics affecting carbon allocation in carbon pools) Seedling establishment (affecting ratios of carbon allocation in carbon pools) Reduction of leaf area due to light competition (affecting photosynthesis) Water competition (affecting transpiration and photosynthesis of each life-form)		
Fire	Consumption of dead aboveground carbon (affecting soil C, nutrient return and soil N pools) Consumption of grass and tree leaf carbon Post-fire mortality of trees (affecting all carbon pools) Consumption of NPP (affecting carbon allocations in carbon pools)	Mortality of seeding (affecting establishment) Consumption of NPP (affecting reproduction)	

heartwood pools for trees and into foliage and roots for grasses (Table 1, Fig. 1). In addition, the C and N associated with litter were separated from soil organic matter into a new litter pool. We also modified the original configuration of TEM so that TEM-LPJ was able to simultaneously consider the dynamics of multiple PFTs.

Production. Carbon assimilation in TEM-LPJ is represented by gross primary production (GPP). The flux GPP is a function of the maximum rate of C assimilation modified by several scalars and is expressed as:

$$GPP = C_{\max} \times FPC \times f(\text{LEAF}) \times f(\text{PAR}) \times f(\text{T}) \times f(\text{CO}_2, \text{H}_2\text{O}) \times f(\text{NA}) \quad (1)$$

where C_{\max} is the maximum rate of C assimilation, FPC is foliage projected cover, $f(\text{LEAF})$ is the phenological model that describes seasonal changes of the vegetation capacity to assimilate C and is relative to maximum annual leaf area, $f(\text{PAR})$ is a function of photosynthetically active radiation, $f(\text{T})$ is a function of the mean monthly air temperature, $f(\text{CO}_2, \text{H}_2\text{O})$ is a function of leaf conductance that depends on atmospheric CO_2 and moisture availability, and $f(\text{NA})$ is a function of N availability. The scalar FPC, which is a concept incorporated from LPJ, represents the conversion of leaf area index (LAI) based on Beer's law (see Haxeltine 1996) and is used to describe the effect of foliage

development on gross primary production.

Net primary productivity (NPP) is calculated as the difference between gross primary production (GPP) and plant respiration (R_A) (see Fig. 2). Based on the allocation equations of LPJ, a portion of NPP is used for reproduction, and the remainder is allocated to the different vegetation C pools (Table 3). The allocation of C to the leaf and root pools is critical to competition for light and water among the PFTs (Fig. 1).

Nitrogen cycling. In TEM-LPJ, the C and N cycles are coupled so that aspects of the N cycle influence C dynamics. The N cycle influences C assimilation (GPP) through the scalar $f(\text{NA})$ in Eq. 1, which scales back GPP by the amount of N available for tissue construction (McGuire et al. 1992; Pan et al. 1998). The N available for tissue construction is determined by the sum of N uptake from the available N pool (NUPTAKE_L and NUPTAKE_S in Fig. 2) and the amount of N that can be mobilized from plant storage (NMOBIL in Fig. 2). In TEM, net N mineralization (NETNMIN in Fig. 2) associated with decomposition of detritus recycles N to the available N pool (N_{AV} in Fig. 2) to influence C dynamics of the ecosystem through N uptake by the vegetation. Decomposition is represented as heterotrophic respiration (R_H), which is a function of soil C storage, soil moisture, air temperature, and litter-fall N content

Table 3. Additional model description.

1. Carbon allocation

Vegetation carbon is divided into four pools for tree and two pools for grass PFTs. Trees pools include leaf C (C_l), sapwood C (C_{sw}), heartwood C (C_{hw}), and root C (C_r). Grasses pools include leaf C (C_l) and root C (C_r). Besides 20 % of annual NPP allocated to reproductive effort; the remaining NPP is allocated to the carbon pools based on the following partitioning ratios:

for trees:

$$P_l/P_r = \lambda \times W_s \quad (1.1a)$$

$$P_{sw} = 10 \times P_l \quad (1.1b)$$

$$P_l + P_r + P_{sw} = 1 \quad (1.1c)$$

for grasses:

$$P_l/P_r = \lambda \times W_s \quad (1.2a)$$

$$P_l + P_r = 1 \quad (1.2b)$$

where P_l , P_r , and P_{sw} are the proportions of NPP allocated to C_l , C_r , and C_{sw} respectively. λ is a partitioning ratio that varies for different PFTs (1.5 for tree and 0.7 for grass PFTs). λ is modified by an index of water stress (W_s). As a PFT becomes more water stressed (a reduction of W_s), the PFT allocates proportionally more biomass to roots in order to have sufficient access to soil water (Grime et al. 1984). For trees, equation A1.1b assumes that sapwood plays a role in water transport to the leaves as described by the pipe-model (Shinozaki et al. 1964a, b). During the growing season, the status of water stress is checked every month. If water stress causes a smaller ratio of leaf mass and sapwood than the previous month, leaf mass is reduced. To maintain the ratio between leaf mass and sapwood under such a drought, part of the sapwood will turn to heartwood while the rest sapwood keeps functioning to support the remaining leaf mass.

The portion of annual NPP used for reproductive effort may first be reduced by some factors such as mortality and fire. The remaining carbon is then allocated to the tree or grass vegetation pools assuming that new plants use different allocation ratios than mature plants:

for trees:

$$P_{newl} = P_{newr} \quad (1.3a)$$

$$P_{newsw} = 10 \times P_{newl} \quad (1.3b)$$

$$P_{newl} + P_{newr} + P_{newsw} = 1 \quad (1.3c)$$

for grasses:

$$P_{newl} = P_{newr} \quad (1.4a)$$

$$P_l + P_r = 1 \quad (1.4b)$$

where P_{newl} , P_{newr} , and P_{newsw} are the proportions of NPP allocated to new foliage, roots and sapwood respectively.

2. Two-layer soil water model

The percolation function is based on an empirical equation adapted from Neilson (1993, 1995; see also Haxeltine 1996) and is expressed as:

$$P_{erc} = k [w_1 / w_{hc}]^4 N_m \quad (2.1)$$

where P_{erc} is the daily percolation from the upper to lower soil layer; k is an empirical percolation coefficient that depends on soil texture; w_1 is the available soil water in the upper soil layer, w_{hc} is the water holding capacity, and N_m is the number of days of each month and used to aggregate daily percolation to monthly resolution. Soil moisture storage is updated in a monthly step:

$$w_1 = w_1 + R + S_m - P_{erc} - \beta_1 \text{ AET} \quad (2.2a)$$

$$w_2 = w_2 + P_{erc} - \beta_2 \text{ AET} \quad (2.2b)$$

where w_1 and w_2 describe available soil water in the upper and lower soil layers, respectively; R is monthly rainfall; S_m is monthly snowmelt; P_{erc} is monthly percolation from the upper to the lower soil layer; AET is total evapotranspiration and β_1 and β_2 are the extraction rates of transpired water from the upper and lower soil layers (i.e. $\beta_1 + \beta_2 = 1.0$). The extraction rates represent fractions of available water distributed in different soil layers and are calculated as:

$$\beta_1 = w_1 / (w_1 + w_2) \quad (2.3a)$$

$$\beta_2 = w_2 / (w_1 + w_2) \quad (2.3b)$$

3. Rooting depth

The rooting depth depends on soil texture and is calculated based on the equation:

$$R_D = (R_{Da} P_{sic}^2) + (R_{Db} P_{sic}) + R_{Dc} \quad (3.1)$$

where R_D is rooting depth in m and R_{Da} , R_{Db} , and R_{Dc} are the vegetation-specific parameters in the second-order relationship, and P_{sic} is proportion of silt plus clay in the soil profile. For the forest PFTs, we use the values 0.000, -2.0875 and 2.8977 for R_{Da} , R_{Db} and R_{Dc} ; and for the C₃ grassland PFT, we use the values -4.721, 4.106 and 0.3003 for R_{Da} , R_{Db} and R_{Dc} , respectively.

4. Root competition for water

A root extraction index was defined for each PFT in each of the two soil layers [i.e. $R_{E11}(i)$ and $R_{E12}(i)$]. When the total R_{E11} (or R_{E12}) among all PFTs is < 1.0 , there is no competition for water, otherwise water competition occurs among the PFTs. The root extraction indices are calculated as a function of root distribution ratios in the top and lower soil layers, root surface extraction efficiency, root biomass, and a foliage weighting index:

$$R_{E11}(i) = 1.0 - \exp(-0.5 \times R_1(i) + k) \quad (4.1a)$$

$$R_{E12}(i) = 1.0 - \exp(-0.5 \times R_2(i) + k) \quad (4.1b)$$

$$R_1(i) = R_{dr1}(i) \times R_{eff}(i) \times C_r(i) \times \text{FPC}_{in}(i) \quad (4.1c)$$

$$R_2(i) = R_{dr2}(i) \times R_{eff}(i) \times C_r(i) \times \text{FPC}_{in}(i) \quad (4.1d)$$

$$\text{FPC}_{in}(i) = \text{FPC}(i) / \text{Total FPC} \quad (4.1e)$$

where $R_{E11}(i)$ and $R_{E12}(i)$ are root extraction indices that represent the capability of roots to extract water from the top and lower soil layers for PFT i , k is a constant (0.25) based on calibration, $R_1(i)$ and $R_2(i)$ represent water extraction from the top and lower soil layers for PFT i , $R_{dr1}(i)$ and $R_{dr2}(i)$ are root distribution ratios in the top or lower soil layer for PFT i , $R_{eff}(i)$ is root extraction efficiency for PFT i , $C_r(i)$ is root biomass carbon of PFT i , and $\text{FPC}_{in}(i)$ is the FPC weighting index for PFT i , $\text{FPC}(i)$ is the foliage projected cover for PFT i , and Total FPC is sum of FPCs among all PFTs. In TEM-LPJ, 99% of grass roots are distributed in the upper soil layer and 35% of tree roots distributed in the top layer and the rest in the lower soil layer. Root surface extraction efficiency is assigned as 1.0 for grasses and 0.125 for trees, which indicates that grasses have a greater efficiency than trees because of their finer roots.

For a PFT, available water supply $WS(i)$ for extraction is expressed as:

$$WS(i) = P_{R1}(i) w_1 + P_{R2}(i) w_2 \quad (4.2a)$$

where w_1 and w_2 are same as in A2, $P_{R1}(i)$ and $P_{R2}(i)$ are proportions of available water the PFT can get separately from the upper and lower soil layers and are expressed as:

$$P_{R1}(i) = R_{E11}(i) \text{ when } \Sigma R_{E11}(i) \leq 1.0 \quad (4.2b)$$

$$P_{R1}(i) = R_{E11}(i) / \Sigma R_{E11}(i) \text{ when } \Sigma R_{E11}(i) > 1.0 \quad (4.2c)$$

and, $P_{R2}(i) = R_{E12}(i) \text{ when } \Sigma R_{E12}(i) \leq 1.0$ (4.2d)

$$P_{R2}(i) = R_{E12}(i) / \Sigma R_{E12}(i) \text{ when } \Sigma R_{E12}(i) > 1.0 \quad (4.2e)$$

(McGuire et al. 1997). In TEM-LPJ, soil C and N pools are tracked separately for each PFT. Therefore, the competition for soil N between trees and grasses is implicit and occurs through indirect effects of production on soil N pools while production is affected by competition for light and water among the PFTs.

Hydrology. Hydrological characteristics are determined by the water balance model (WBM, Vörösmarty et al. 1989), which was modified based on the two-layer soil water model of LPJ (Table 3). Potential evapotranspiration (PET) is calculated as a function of air temperature, radiation balance and moisture content of evaporating surfaces. Soil moisture is determined from interactions

among rainfall, snowmelt recharge and PET. Evapotranspiration (AET) is calculated based on PET and total available water in the soil profile. Whenever field capacity is attained, excess water is transferred to runoff pools and runoff is generated as a linear function of the existing pool size (Thornthwaite & Mather 1957). The two-layer soil water model of Haxeltine et al. (1996) was combined with the WBM in TEM so that PFTs could compete for water in the two layers. Monthly precipitation and snowmelt minus soil surface evaporation are added to the top soil layer. Water is then redistributed through percolation from the upper soil layer to the lower layer through a function that depends on soil texture (Table 3). Surface runoff and drainage occur separately in the top and lower soil layers when available water exceeds field capacity. In TEM-LPJ, different PFTs share the same soil water pools. Transpiration is calculated for each PFT and each soil layer with the constraint that total transpiration for the ecosystem cannot exceed PET. In TEM, rooting depth of each PFT is the function of soil texture (McGuire et al. 1995b; Table 3). We defined the depth of the upper soil layer as the rooting depth of grasses and the depth of lower layer as the rooting depth of woody plants minus the rooting depth of grasses. Grasses can only extract water from the upper soil layer, and woody plants can extract water from both the upper and lower soil layers.

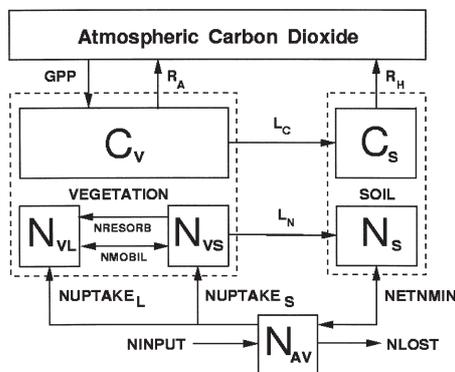


Fig. 2. The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in the vegetation (C_V); structural nitrogen in the vegetation (N_{VS}); labile nitrogen in the vegetation (N_{VL}); organic carbon in soils and detritus (C_S); organic nitrogen in soils and detritus (N_S); and available soil inorganic N (N_{AV}). Arrows show carbon and nitrogen fluxes: GPP, gross primary productivity; R_A , autotrophic respiration; R_H , heterotrophic respiration; L_C , litterfall C; L_N , litterfall N; $NUPTAKE_S$, N uptake into the structural N pool of the vegetation; $NUPTAKE_L$, N uptake into the labile N pool of the vegetation; $NRESORB$, N resorption from dying tissue into the labile N pool of the vegetation; $NMOBIL$, N mobilized between the structural and labile N pools of the vegetation; $NETNMIN$, net N mineralization of soil organic N; $NINPUT$, N inputs from outside the ecosystem; and $NLOST$, N losses from the ecosystem (McGuire et al. 1993).

Vegetation dynamics

LPJ is a global DGVM (Sitch 2000), based on the equilibrium biogeography model BIOME3 (Haxeltine et al. 1996). BIOME3 is a mechanistically based biogeography model that uses a series of ecophysiological constraints and resource limitations as threshold rules to determine the potential occurrence of PFTs (Haxeltine & Prentice 1996). In addition to these features, LPJ also simulates the effects of reproduction, establishment, light competition, water competition and fire disturbance on vegetation dynamics (Sitch 2000). Although LPJ includes C and water dynamics, the model does not consider N cycling. Therefore, in TEM-LPJ, we incorporated only those features from LPJ that represent ecosystem structural dynamics, and relied on TEM to represent biogeochemical processes in the model.

Reproduction. The reproduction module in LPJ defines a fixed proportion of the NPP that is transferred to reproduction organs when plants reach reproductive maturity. Many studies indicate that the amount of photosynthate used for reproduction varies considerably within and among PFTs. Among trees, it has been documented to range from 5% to 35%, and there is a greater range among herbaceous plants (Larcher 1980). We chose a mean value of 20% as amount of annual NPP allocated to reproduction, i.e. a reproductive effort C pool, when plants reach reproductive maturity. Grasses are considered to reproduce every year, and woody plants start to reproduce when FPC exceeds 50%.

Establishment. Seed germination and seedling establishment occur in forests when there is exposed soil, an adequate supply of viable seeds, and appropriate environmental conditions (Kozłowski et al. 1991). In TEM-LPJ, establishment is represented by allocating the C in the reproductive effort pool into the vegetation C pools after reductions to account for the effects of seed and sapling mortality. For grasses, no reductions are assumed to occur and the entire reproductive effort pool is allocated equally to foliage and roots each year (Table 3). For trees, however, the reproductive effort pool is reduced by 50% because of the high mortality of seeds (Kozłowski et al. 1991) and further reduced by 80% when simulated fire occurs in TEM-LPJ because ground fires can cause seedling mortality of woody plants (Daubenmire 1968). The remaining C is then allocated to foliage, roots and sapwood based on NPP allocation patterns of saplings (Table 3). With these allocations, the effects of saplings for each PFT could be accounted for in competition for light and water resources.

Competition for light. Populations of trees compete with

understorey shrubs and herbaceous plants for available light resources. Competition may be one-sided, with large plants decreasing the growth of small neighbours but not vice versa, or it may result in mutual inhibition of growth by competing plants (Cannell et al. 1984). In TEM-LPJ, total FPC is constrained so that it does not exceed 1.0. When the sum of FPC across all PFTs is less than 1.0 light competition does not occur. When the sum of FPC is calculated to exceed 1.0 the trees are considered to have a competitive advantage over grasses. Thus, the FPC of grasses is reduced so that total FPC does not exceed 1.0. When light competition occurs among different woody types, the equivalent proportion of FPC is reduced for each type to meet the FPC constraint (Sitch 2000).

Competition for water. Plants compete for water and nutrients based on the extent of each plant's root system and its depth, density, and capacity to absorb water and mineral nutrients (Connor 1983). In TEM-LPJ, we considered four factors affecting water competition: root distribution ratios in the top and lower soil layers (effect of rooting depth), root surface extraction efficiency (effect of capacity to absorb water), root biomass (effect of root density), and foliage index (effect of leaf area on the potential to extract water from soils). The root extraction index (R_{EI}) of each PFT for each soil layer is a scalar that is determined from a function that depends on these factors, and a relationship between root efficiency and root density (Jackson et al. 1996). Root competition for water in the same soil layer occurs when R_{EI} summed across PFTs is greater than 1.0. In this case, available water for a PFT is determined as a fraction of total available water calculated as the ratio of the PFT R_{EI} to the total R_{EI} in the soil layer (Table 3).

Fire

Fire is one of the most dramatic forces that alter forest ecosystems (Kozlowski et al. 1991). There are two fire modules in LPJ that were incorporated into TEM-LPJ to describe fire frequency and effects of fire disturbance:

Fire frequency. The fire frequency module predicts the fraction of land area affected by fire in a given year. The reciprocal of this quantity describes the fire return interval. Calculation of the fire frequency depends on fuel load and fuel moisture:

$$F_f = (\sum \beta_i (f_{Li})^2)(1 - \exp(-\eta n_{dd})) \quad (2)$$

where F_f is the fire frequency, f_{Li} is the fuel load for PFT i , n_{dd} is the number of dry days, β_i is the flammability parameter for PFT i , and η is a constant (defined by

Sitch 2000). Ignition sources, e.g., lightning, are considered to be available throughout the year and do not limit fire frequency in this implementation. The fuel load of woody plants includes the litter layer, while the fuel load of grasses includes both live shoots and litter. Fuel load for each PFT is calculated from the C pools simulated by the biogeochemical model. The fuel load is summed across PFTs and then multiplied by a flammability parameter (β_i) specified for each PFT. Grass is considered more flammable than woody plants and the presence of the grasses encourages the propagation and higher intensity of a fire once ignited (Daubenmire 1968). The effect of fuel moisture is calculated as the fraction of dry days over the year where litter moisture content is lower than the level that is capable of extinguishing ignited fires. The extinguishing moisture content is defined as 15% volumetric soil moisture, a drought threshold at which predawn water potential of trees starts to dramatically decrease (Waring & Schlesinger 1985). When moisture is above this limit, litter is assumed to be too damp to ignite fire and to propagate fire to a significant distance.

Fire disturbance. The fire disturbance module predicts the effect of fire on the C and N pools and the leaf area of each PFT based on algorithms for fire intensity, fire frequency (described earlier), and post-fire mortality. Fire intensity, which is calculated as the function of total fuel mass divided by the mean annual litter moisture content, determines whether a ground fire or a more destructive crown fire occurs. A fire disturbance reduces the litter pools of each PFT, and reduces the above-ground vegetation C pool of grass PFTs for ground fires and of woody PFTs for crown fires. The post-fire mortality of woody plants is proportional to the square of the fire frequency (Sitch 2000) and promotes further reductions of the C pools of woody plants. It is assumed that no grass dies due to fire disturbance. Because changes

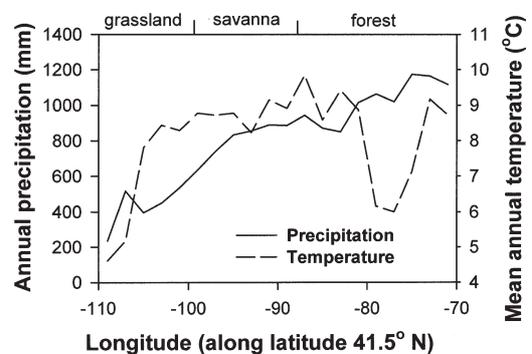


Fig. 3. Annual precipitation (mm) and mean annual temperature (°C) along a moisture transect at 41.5° N latitude in the United States.

in C pools due to fire disturbance affect LAI and root density of PFTs, fire disturbance also influences light and water competition among PFTs.

Methods

Model parameterization and evaluation

After developing TEM-LPJ, we parameterized the model for three plant functional types: a temperate deciduous forest, a temperate coniferous forest, and a temperate C_3 grassland. The temperate deciduous and coniferous forest parameterizations were based on field data from a mixed hardwood stand and from a *Pinus resinosa* plantation, respectively, studied by the Harvard Forest Long Term Ecological Research (LTER) program in Petersham, Massachusetts. The grassland parameterization was based on field data from the Pawnee National Grasslands, which has been studied by the Central Plains Ecological Research LTER program in northeastern Colorado. The field data for developing these parameterizations have previously been described in McGuire et al. (1992).

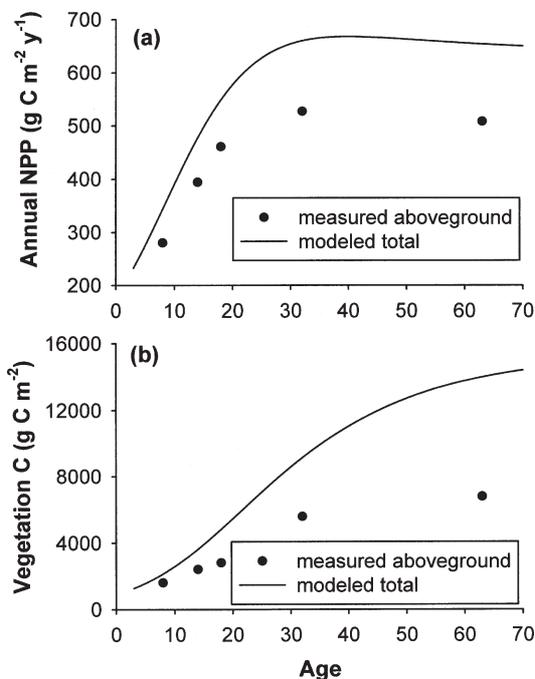


Fig. 4. Measured above-ground and simulated total (a) annual net primary production (NPP) and (b) vegetation carbon for *Populus tremuloides* in central Wisconsin. Simulations were conducted by using a deciduous plant functional type parameterized at the Harvard Forest in Massachusetts.

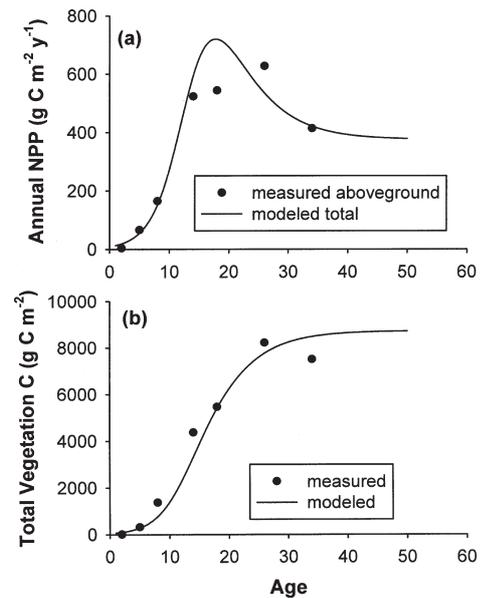


Fig. 5. a. Measured above-ground annual net primary production (NPP) compared with simulated total annual NPP; b. Measured total vegetation carbon compared with simulated total vegetation carbon for *Pinus eliottii* in Florida. Simulations were conducted by using a coniferous plant functional type parameterized at the Harvard Forest in Massachusetts.

To evaluate the model, we examine the ability of TEM-LPJ to simulate several aspects of ecosystem function and structure. First, we compare our simulated age-dependent changes in NPP and vegetation C storage for temperate deciduous and coniferous forests with comparable data collected at a chronosequence of *Populus tremuloides* stands in Wisconsin and a chronosequence of *Pinus eliottii* stands in Florida, respectively. We then examine how well model simulations of competition dynamics between deciduous trees and grasses predict the composition of PFTs at three sites experiencing different environmental conditions (i.e., a temperate deciduous forest site, a temperate savanna site, and a grassland site). Finally, we compare model estimates of NPP, percent foliar cover, and vegetation C of deciduous tree and C_3 grassland PFTs along a moisture gradient (an east-west transect at 41.5° N from the east coast of the United States to the western Great Plains) to boundaries of potential vegetation types defined by VEMAP Members (Anon. 1995) to examine the ability of TEM-LPJ to simulate spatial changes in both ecosystem structure and function across an environmental gradient. We expect that on the wetter end of the gradient, light competition will be more important than water competition so that trees will tend to dominate along the east coast of the United States. However, as environmental conditions become drier, water competition will become progressively more important and grasses will

become more dominant as one moves into the western Great Plains.

Study sites and data description

We evaluated the age-dependent C dynamics of the deciduous and coniferous forest PFTs by comparing model simulations to stand-level data on age-dependent NPP and vegetation C. The simulation of the deciduous PFT was evaluated with data from a *Populus tremuloides* stand in Wisconsin (see Ruark & Bockheim 1988), and the simulation of the coniferous forest PFT was evaluated with data from a *Pinus elliotii* plantation in Florida (see Gholz & Fisher 1982). The climate, soil texture and elevation data used to drive the model simulations were derived from the VEMAP data sets (Kittel et al. 1995) for the grid cells (0.5° latitude by 0.5° longitude) that contained the *Populus tremuloides* and *Pinus elliotii* sites. The VEMAP climate data sets represent long-term means for the conterminous United States.

For evaluating competition dynamics simulated by the model using both the deciduous forest and grass PFTs, we chose the Harvard Forest as a site representative of temperate deciduous forest, a site located in the tree-grass ecotone as representative of temperate savanna, and the Pawnee Grassland as a site representative of grassland. Climate and soil data for Harvard Forest and the Pawnee Grassland were derived from site measurements, and data for the savanna site were derived from the VEMAP data sets. For simulations along the transect at 41.5° N latitude in the conterminous United States, we selected grid cells ($0.5^\circ \times 0.5^\circ$) at intervals of 2° longitude and derived the input data from the VEMAP data sets (see Fig. 3 for data on annual precipitation and mean annual temperature).

Application of TEM-LPJ

To apply TEM-LPJ, the model requires information on elevation, soils, climate, candidate PFTs, and soil- and PFT-specific parameters. For the simulations in this study, the initial values for C and N pools of vegetation and soil of a PFT were 1% of the equilibrium values from the parameterization for the PFT. In each application of the model in this study, the simulations were conducted for 120 years. None of the simulations considered inter-annual variability in climate, but the climate data sets did contain seasonal variation in temperature, precipitation, and cloudiness. Because the model is run under the same mean climate year by year, fire can occur only in the area where the fuel-load and fuel moisture meet the requirement for fire occurrence. Therefore, fire disturbance occurs annually for some locations and represents the mean long-term effect of

fire rather than an event that occurs in association with climate variability. As a result, these applications of TEM-LPJ are only used for evaluating model dynamics and should not be considered representative of the historical fire regime.

Results

For the *Populus tremuloides* site, the application of the deciduous forest PFT simulated total annual NPP and total vegetation C storage that follow the shape of the age-dependent pattern of measured above-ground NPP and above-ground vegetation C storage (Fig. 4). At age 70, the modeled total annual NPP is approximately 20% higher than above-ground annual NPP. In contrast, modeled total vegetation C is ca. 50% more than above-ground vegetation C. If the total annual NPP and vegetation C storage simulated by the model are representative of the sites, these results suggest that while most of NPP is allocated above-ground, turnover of below-ground vegetation C must be slower than above-ground C. For the *P. elliotii* site, the application of the coniferous forest PFT simulates total annual NPP and total vegetation C storage that follows the shape of the age-dependent pattern of measured above-ground annual NPP and total vegetation C (Fig. 5). The simulation of total annual NPP suggests that either the model is underestimating allocation to roots or that the allocation to roots is quite small. The simulation of total vegetation C is similar to measured total vegetation C. Taken together, the applications of the deciduous forest and coniferous forest PFTs indicate that TEM-LPJ can simulate stand development in a reasonable fashion in climatically diverse sites.

The simulations of competition between deciduous forest and C_3 grass PFTs for climates characteristic of temperate deciduous forest, temperate savanna and grassland illustrate the effects of competition for water and light resources between the deciduous forest and grass PFTs in the different environments (Fig. 6). At the deciduous forest site, grasses dominate annual NPP (Fig. 6a) and FPC (Fig. 6b) early in succession with grass leaf area peaking within the first 20 yr and then declining through the remainder of the simulation as trees shade out the grass. In contrast, at the grassland site the grass PFT dominates NPP (Fig. 6e) and FPC (Fig. 6f) throughout the simulation as the grass PFT outcompetes the tree PFT for water resources. At the temperate deciduous savanna site, grasses dominate both annual NPP (Fig. 6c) and FPC (Fig. 6d) through much of the 120 year simulation as trees grow slowly in the dry climate and take more than 80 years to cover 50% of site area with their foliage (Fig. 6d). In comparison to the

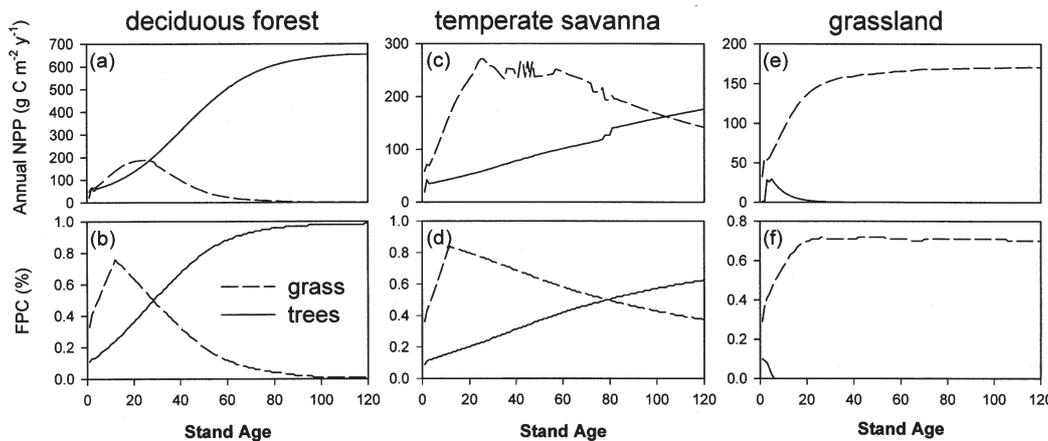


Fig. 6. Simulated successional patterns of primary production (a, c, e) and foliage projected cover (FPC; b, d, f) interactive between deciduous forest (solid line) and grass (dashed line) plant functional types at sites representative of temperate deciduous forest (a, b), temperate savanna (c, d), and grassland (e, f) in the United States.

deciduous forest site, NPP of trees in the temperate deciduous savanna site is low at the end of the simulation ($< 200 \text{ g C m}^{-2}$; Fig 6c).

For the simulations along the transect at 41.5° N , the composition of the simulated ecosystems along the length of the transect corresponds to the boundaries between potential temperate deciduous forest, temperate savanna, and grassland, as defined by VEMAP Members (Anon.

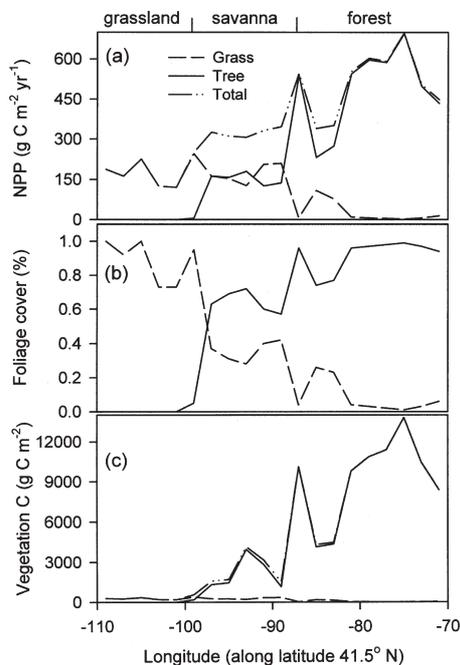


Fig. 7. a. Annual net primary production (NPP); **b.** Foliage projected cover (FPC) and **c.** Vegetation carbon for the application of TEM-LPJ along a moisture transect at 41.5° N in the United States using deciduous forest and grass plant functional types.

1995) (Fig. 7). East of 88° W , the deciduous forest PFT dominates NPP (Fig. 7a), FPC (Fig. 7b), and vegetation C (Fig. 7c), and west of 96° W , the grassland PFT dominates NPP, FPC, and vegetation C. Domination by deciduous forest in the east is the result of competition for light, whereas domination by grass in the west is the result of competition for water. In the temperate savanna region between 88° W and 96° W , the NPP of the deciduous forest and grass PFTs is similar, FPC of the deciduous forest PFT tends to be larger than FPC of the grass PFT, and the deciduous forest PFT dominates vegetation C (Fig. 7). Some of the variation in FPC in the transition zone between temperate deciduous forest and temperate grassland is associated with soil texture, which affects water competition between the deciduous forest and grass PFTs.

Discussion

Our strategy in this paper was to combine features from a biogeochemistry model that considers how interactions among C, N, and water influence ecosystem biogeochemistry and from a DGVM that considers how interactions among water and light influence structural dynamics of ecosystems. After combining the features of these two models, our approach was to evaluate the age-dependent growth dynamics of single forest PFTs and to evaluate tree-grass interactions. These evaluations revealed both strengths and limitations of TEM-LPJ, and identified issues that need to be considered in further developing the model.

Age-dependent growth dynamics

Many successional models focus on the demographic processes of species within a single PFT during succession (e.g. the gap models of Shugart & West 1980). We were interested in evaluating whether a PFT-level parameterization could capture biogeochemical dynamics through succession without considering each individual species within the PFT. Our application of the deciduous and coniferous forest PFTs, which were parameterized for stands at the Harvard Forest, adequately represented the age-dependent NPP and vegetation C at deciduous and coniferous forest sites at some distance from the Harvard Forest. For the *P. elliotii* site, the model was also able to capture age-dependent decline in NPP, a phenomenon that has been observed in many forest stands as trees age. Several hypotheses exist to explain this phenomenon (Gower et al. 1996), and there is currently much research focused on testing these hypotheses. Although more testing of the parameterizations for deciduous and coniferous forest PFTs in TEM-LPJ is needed to determine whether they are robust across different deciduous and coniferous forest species in eastern North America, the evaluation of the performance of the age-dependent C dynamics in this study has led to a version of TEM that is able to consider the effects of cropland abandonment and subsequent forest regrowth on global terrestrial C dynamics (McGuire et al. 2001).

Tree-grass interactions

Our evaluation of tree-grass interactions simulated by TEM-LPJ indicated that light competition led to dominance by the deciduous forest PFT in moist regions of eastern United States and that water competition led to dominance by the grass PFT in dry regions of the central United States. The estimates of annual NPP and vegetation C simulated by the model along the transect at 41.5° N are similar to results reported by VEMAP Members (Anon. 1995). Although the simulation results for the deciduous forest and grassland regions led to stable solutions, the simulation for the temperate savanna region elucidated some aspects of model behaviour that challenge our representation of tree-grass interactions in the model.

Savannas are regions where trees and grasses co-exist (Scholes & Archer 1997). Walker & Noy-Meir (1982) and Scholes & Archer (1997) proposed different hypotheses to explain the co-existence of trees and grasses in savannas. The hypothesis of Walker & Noy-Meir (1982) relies on the partitioning of water resources among trees and grasses in savannas; grasses have access to soil moisture near the surface and trees have access to deeper

soil moisture. In contrast, the hypothesis of Scholes & Archer (1997) proposes that fire is an important factor promoting co-existence of the two life forms in which fire kills tree seedlings and prevents trees from shading out grasses. Daubenmire (1968) also proposed that without fire trees will replace grasses in a savanna. Other studies suggest that trees and grasses do compete for water in savannas (Belsky 1994; Jackson et al. 1996).

TEM-LPJ incorporates features of these hypotheses in simulating tree-grass interactions in savannas. Ancillary analyses with the model revealed that simulated dynamics of trees and grasses are quite sensitive to distribution of tree roots between the top and lower soil layers. Also, our simulations indicated that trees will eventually shade out grasses in savannas, and that changing the distribution of tree roots primarily changes the length of time for trees to shade out grasses. To maintain co-existence of trees and grasses in temperate savannas, it is not clear whether the representation of fire disturbance in the model needs to be altered or if the model needs to be driven with climate that has inter-annual variability.

Nitrogen dynamics

Although we combined features of TEM and LPJ to develop a model that simultaneously considers interactions among C, water, and N, the current structure of the model, in which soil pools are tracked by PFT, does not allow us to fully consider interactions among PFTs for N. Although the approach we took in this study may be a reasonable first-order approximation for savanna ecosystems as many observations suggest that competition for water is important in savannas and that nutrient uptake may be closely related to water uptake (Chapin et al. 1987), there are several interactions for N that require a model structure in which all PFTs are competing for the same available N in the soil. For example, nutrients accumulating below trees may benefit the growth of grasses under savanna tree canopies (Weltzin & Coughenour 1990). The effects of disturbance on N dynamics also has important implications for tree-grass dynamics during succession in eastern-deciduous forests (Marks 1974). Substantial nutrient losses occur after disturbance in eastern deciduous forests as a result of ongoing decomposition because of insufficient plant uptake of nutrients (Bormann et al. 1974), and soil organic matter decreases until sufficient plant growth occurs so that inputs to the soil exceed losses from decomposition (Covington 1981; Waring & Schlesinger 1985). Clearly, to capture the effects of these post-disturbance N dynamics on successional C dynamics, PFTs need to compete for N in a soil that is shared among the PFTs.

While the consideration of interactions with N dy-

namics is incomplete, the evaluation in this study reveals that (1) the model appears capable of representing the age-dependent growth of deciduous and coniferous forest stands in eastern North America with PFT-level parameterizations, and (2) the model simulated a reasonable pattern of C dynamics and PFT composition along a moisture transect from the central Great Plains to the Atlantic Ocean in the temperate United States. Further development of the model requires evaluating simulated fire disturbance dynamics in the temperate savanna region of the United States, considering the effects of inter-annual variability on fire disturbance, modifying the model so that PFTs compete for N in a soil layer that is shared among the PFTs, and testing the model in other regions. Finally, the applicability of any global dynamic vegetation model for examining contemporary changes in ecosystem function and structure will be limited if the model only simulates potential vegetation. Thus, future development of these models should include the effects of various human disturbances on ecosystem function and structure.

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