A dynamic global vegetation model for use with climate models:
concepts and description of simulated vegetation dynamics

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Abstract

Changes in vegetation structure and biogeography in response to climate change have important feedbacks on climate. In this paper, we describe an approach in which ecological concepts from the Lund-Potsdam-Jena dynamic global vegetation model (LPJ-DGVM) are added to the NCAR Land Surface Model (NCAR LSM) to grow plants in a climate model. Vegetation is represented as spatially independent patches of plant functional types (PFTs). Each PFT is represented by an individual plant with the average biomass, crown area, height, and stem diameter (woody plants only) of the PFT population, by the number of individuals in the population, and by the fractional cover in the grid cell. The coupled LSM-DGVM model has three time-scales. Surface fluxes of energy, moisture, momentum, and CO₂ occur at a 20-minute time-step, updating the hydrologic cycle and soil temperature every time-step. Carbon is accumulated annually and used to update PFT mass, density, and coverage once a year in response to establishment, resource competition, growth, mortality, and fire. Leaf area index is updated daily to a maximum value set by the annual vegetation dynamics. The coupling approach is successful. The model simulates global biogeography and biome-average net primary production that are consistent with observations. The model also simulates dynamics of tundra, boreal forest, northern hardwood forest, tropical rainforest, and savanna ecosystems that are consistent with observations. This suggests that the LSM-DGVM model can be used with a climate model to study biogeophysical feedbacks in the climate system related to vegetation composition and structure.
Introduction

Terrestrial ecosystems affect climate through exchanges of energy, water, momentum, CO₂, trace gases, and mineral aerosols. Changes in community composition and ecosystem structure alter the fluxes and in doing so alter climate. Most studies of vegetation feedback on climate have focused on biogeophysical processes related to energy and water.

The importance of vegetation in determining climate is seen in North Africa, where the contrasts between barren and vegetated landscapes in albedo, surface roughness, surface conductance, and soil texture influence precipitation. Increased summer solar radiation 6,000 years ago strengthened the African summer monsoon (Kutzbach & Otto-Bliesner 1982; Braconnot et al. 2000), allowing grasses and shrubs to cover much of the modern Sahara Desert (Hoelzmann et al. 1998; Jolly et al. 1998a,b; Prentice et al. 2000). Climate simulations that use prescribed desert or vegetated surfaces show that the greening of the Sahara results in more precipitation (Kutzbach et al. 1996). The consensus is that the climate of North Africa 6,000 years ago cannot be realistically simulated without vegetation feedback on climate (Joussaume et al. 1999).

Another example is the boreal forest-tundra ecotone. Climate simulations with prescribed vegetation, in which the boreal forest is replaced with tundra or bare ground, show that the boreal forest warms climate, due primarily to vegetation masking of snow albedo (Bonan et al. 1992; Thomas & Rowntree 1992; Chalita & Le Treut 1994; Douville & Royer 1996). Other such studies show that expansion of tundra at the expense of forest may have played a role in the onset of the last glaciation (Gallimore & Kutzbach 1996) and likely reinforced the cold climate of the last glacial maximum 21,000 years ago (Crowley & Baum 1997). As climate warmed, the treeline migrated northwards. The decrease in surface albedo caused by northward expansion of the boreal forest in response to climate warming accentuated the warming, as shown by Foley et al. (1994) during the mid-Holocene.

Global vegetation models have been developed to allow interactive coupling of climate and vegetation (Foley et al. 1998). One approach, known as asynchronous equilibrium coupling, uses relationships between climate and biogeography to interactively change vegetation cover, iterating until a stable climate-vegetation solution is obtained. Studies utilizing this type of coupling show the importance of the treeline in initiating the last ice age (de Noblet et al. 1996), reinforcing the cold high latitude climate of the last glacial maximum (Texier et al. 1997; Kubatzki & Claussen 1998), and reinforcing the mid-
Holocene high latitude warming (Texier et al. 1997; Kubatzki & Claussen 1998). Other studies show that the greening of the Sahara enhances the summer monsoon 6,000 years ago (Claussen & Gayler 1997; Texier et al. 1997; de Noblet-Ducoudré et al. 2000) and that the choice of initial vegetation cover of desert or forest can lead to different simulated climate (desert-dry, forest-wet) in the western Sahara (Claussen 1994, 1997, 1998; Claussen et al. 1998; Kubatzki & Claussen 1998).

Another class of models, known as dynamic global vegetation models, simulates transient vegetation dynamics (Foley et al. 1998, 2000). The Integrated Biosphere Simulator (IBIS) epitomizes the coupling of such a model to a climate model (Foley et al. 1996; Kucharik et al. 2000). One application of IBIS to study the last glacial maximum found that the cold, dry glacial climate reduces forest cover in the tropics and northern latitudes (Levis et al. 1999). Loss of trees cools temperature over much of Eurasia through the snow-vegetation albedo feedback and warms temperature and decreases precipitation in the tropics. Another climate simulation showed that the greater precipitation in North Africa 6,000 years ago is sufficient to sustain a northward encroachment of plants into desert and that this enhances precipitation (Doherty et al. 2000). Simulations with IBIS for a doubling of atmospheric CO₂ from pre-industrial levels show large changes in climate from vegetation changes (Levis et al. 2000). Similar vegetation feedbacks with higher atmospheric CO₂ have been found in another coupled climate-vegetation model (Betts et al. 1997, 2000).

These studies of vegetation feedbacks have focused on biogeophysical processes related to energy, moisture, and momentum exchange with the atmosphere, showing amplification by vegetation of the climate response to changes in insolation or atmospheric CO₂. Biogeochemical feedbacks are only now being included in climate models. For example, the northward expansion of boreal forest into tundra decreases surface albedo and removes carbon from the atmosphere. The climate cooling resulting from lower atmospheric CO₂ concentration may offset the warming from reduced surface albedo (Betts 2000). Claussen et al. (2001) contrasted the biogeophysical and biogeochemical effects of tropical and boreal deforestation. Tropical deforestation warms climate regionally due to reduction in evapotranspiration. Deforestation releases carbon to the atmosphere, resulting in warming that exceeds that from biogeophysical processes. Boreal deforestation cools climate as a result of the snow-vegetation albedo feedback but warms climate from carbon emissions, though not enough to compensate for the
biogeophysical cooling. Another climate model that included vegetation dynamics and oceanic carbon fluxes found dieback of tropical forests as a result of a drier, warmer climate with higher atmospheric CO₂ released carbon to the atmosphere that accentuated the climate change (Cox et al. 2000).

The purpose of this study is to describe a dynamic global vegetation model for use with the Community Climate System Model. The Community Climate System Model is a coupled atmosphere-land-ocean-sea ice model (Blackmon et al. 2001). Critical to inclusion of interactive vegetation is the linking of vegetation dynamics to the land biogeophysical and hydrological processes in the climate model. In this respect, the model is similar in concept to IBIS (Foley et al. 1996; Kucharik et al. 2000). However, the land model is the NCAR Land Surface Model (NCAR LSM) (Bonan 1996, 1998; Bonan et al. 2002) and the vegetation dynamics uses many of the concepts of the Lund-Potsdam-Jena (LPJ) dynamic global vegetation model (Sitch 2000; Cramer et al. 2001; McGuire et al. 2001). This paper describes the model’s simulated biogeography and vegetation dynamics. We emphasize vegetation composition and structure because these control biogeophysical feedbacks, which are our initial research focus. However, we also discuss aspects of the carbon cycle because biogeophysical and biogeochemical feedbacks must ultimately be considered in an integrated modeling framework.
Methods and model description

We followed the IBIS (Foley et al. 1996; Kucharik et al. 2000) approach of integrating atmospheric and ecological processes across multiple time-scales (Figure 1). Surface processes are organized into: biogeophysics and biogeochemistry – the instantaneous exchange of energy, moisture, momentum, and CO₂ with the atmosphere; phenology – the daily emergence and senescence of foliage; and vegetation dynamics – annual changes in community composition and ecosystem structure.

The biogeophysics module is the NCAR LSM (Bonan 1996, 1998; Bonan et al. 2002). It simulates energy, moisture, and momentum exchange with the atmosphere, snow hydrology, soil temperature, and soil water. In addition, photosynthesis and stomatal conductance are linked through the Farquhar et al. (1980) photosynthesis model and the Collatz et al. (1991, 1992) stomatal conductance model (Bonan 1995; Craig et al. 1998).

NCAR LSM represents spatial heterogeneity in land cover by dividing each model grid cell into 5 land cover types: glacier, lake, wetland, urban, and vegetation (Bonan et al. 2002). The vegetated portion of the grid cell is further divided into patches of several plant functional types (PFTs). Multiple PFTs can co-occur in a grid cell so that, for example, a mixed broadleaf deciduous and needleleaf evergreen forest consists of patches of broadleaf deciduous trees, needleleaf evergreen trees, and bare ground. Each patch, while co-occurring in a grid cell, is a separate column for energy and water calculations. Without vegetation dynamics, PFT relative abundance in a grid cell and the height, leaf area, and stem area of each PFT are obtained from satellite data products (Bonan et al. 2002).

The LPJ dynamic global vegetation model (Sitch 2000; Cramer et al. 2001; McGuire et al. 2001) also characterizes vegetation as patches of PFTs and thus provides the ecological principles to grow PFTs in NCAR LSM. LPJ couples fast hydrological and physiological processes and slower ecosystem processes using time-scales of daily (soil water, soil temperature, snow, canopy physiology, phenology), monthly (soil microbial processes), and yearly (vegetation dynamics). We eliminated processes redundant with NCAR LSM (canopy physiology, snow, and soil physics), altered algorithms to meet the requirements of a climate model (phenology), and adapted the daily and monthly respiration to fit the 20-minute time step with which surface fluxes are exchanged with the atmosphere (Figure 1). We retained the daily time step for leaf area and the annual time step for changes in community composition and ecosystem structure.
(Figure 1). New processes in NCAR LSM are net primary production, biomass turnover and litterfall, allocation, mortality, aboveground competition, establishment, fire, phenology, and litter and soil carbon.

Representation of vegetation

Multiple patches of PFTs in a grid cell is an integrating concept for NCAR LSM and LPJ. LPJ divides vegetation into patches of PFTs that are each treated as a homogeneous dynamic unit. Each PFT is represented by an individual plant with the average biomass, crown area, height, and stem diameter (woody plants only) of the PFT population, by the number of individuals in the population, and by the fractional cover in the grid cell. Woody PFTs are divided in foliage, sapwood, heartwood, and fine root carbon pools. Herbaceous PFTs are represented by foliage and fine roots. Properties of the average individual multiplied by population density scale from the individual to the patch. Herbaceous plants have a population density of one so that the individual represents the patch. Patch properties multiplied by fractional cover scale from the patch to the grid cell.

We use 10 PFTs. Two tropical trees, three temperate trees, and two boreal trees are differentiated by bioclimatology, leaf form (broadleaf, needleleaf), phenology (evergreen, summergreen, raingreen), physiology, and response to disturbance. Three grasses are distinguished by bioclimatology and photosynthetic pathway (C\textsubscript{3}, C\textsubscript{4}). These PFTs are as in LPJ, with the exception that we divided C\textsubscript{3} grass into arctic and non-arctic types (Table 1). The PFTs are a sub-set of the 15 PFTs used in NCAR LSM (Bonan et al. 2002). Leaf optics (Table 2), photosynthesis (Table 3), and morphology (Table 4) are standard NCAR LSM parameters. Bioclimatic limits for survival and establishment (Table 1) and additional parameters for vegetation dynamics (Table 5) are as in LPJ except as noted. Without vegetation dynamics, NCAR LSM allows at most 4 PFTs to co-occur in a grid cell. With vegetation dynamics, all PFTs can potentially co-occur depending on climate.

Net primary production

The biomass increment of the average PFT individual is the difference between carbon uptake during gross primary production and carbon loss during maintenance and growth respiration. Gross primary production is calculated every 20-minutes using the NCAR LSM photosynthesis-conductance
parameterization (Figure 1). In calibrating the integrated model, we altered the canopy scaling of photosynthesis. NCAR LSM scales photosynthesis from the leaf to the canopy by calculating photosynthesis separately for sunlit and shaded leaves. Canopy photosynthesis is the sum of these two fluxes weighted by sunlit and shaded leaf area. Photosynthesis by shaded leaves is in relation to the amount of diffuse radiation received. This allows shaded leaves to contribute to gross primary production even in a dense canopy. We altered the canopy scaling so that only sunlit leaves photosynthesize. Values for $V_{\text{max}25}$ for each PFT (Table 3) are consistent with the new canopy scaling and were obtained from published estimates (Wullschleger 1993) and IBIS (Kucharik et al. 2000).

Respiration is calculated every 20-minutes using the LPJ algorithms, but with rate coefficients adjusted to instantaneous rather than daily (Figure 1). Maintenance respiration has a base rate of $6.3426 \times 10^{-7} \text{ g C g N}^{-1} \text{ s}^{-1}$. This is adjusted for tissue C:N ratio (Table 5), a factor that represents acclimation of respiration to the PFT’s bioclimate (Table 5), and temperature. Vegetation temperature controls foliage and stem respiration; soil temperature controls root respiration. After accounting for maintenance respiration, 25% of the remaining carbon is subtracted for growth respiration.

LPJ factors that adjust the base respiration rate for acclimation are 0.2 for the two tropical PFTs and 1.2 for the other PFTs. We increased this to 0.5 for tropical PFTs and reduced it to 0.6 for boreal PFTs (Table 5). This was necessary because of the high $V_{\text{max}25}$ of tropical trees and the low $V_{\text{max}25}$ of boreal trees (Table 3). Presumably, differences in photosynthetic capacity should be reflected in leaf nitrogen (which also affects maintenance respiration), but we kept C:N ratios constant among PFTs as in LPJ (Table 5).

**Litter and soil carbon**

Heterotrophic respiration is calculated over 20-minutes using LPJ’s formulation of two litter carbon pools (above- and belowground) for each PFT and two soil organic carbon pools (fast and slow). The rate of decomposition depends on litter quality, soil temperature, and soil moisture. The nitrogen cycle is not included. Carbon loss is summed annually so that carbon pools are updated once per year for litterfall and decomposition (Figure 1).
**Biomass turnover and litterfall**

Biomass turnover occurs annually (Figure 1) and is inversely proportional to a turnover period (Table 5). Foliage and root turnover contribute to annual litterfall. Sapwood turnover accumulates as heartwood. Heartwood is transferred to aboveground litter upon mortality or is consumed during fire.

**Allocation**

Net primary production is summed annually to update carbon pools (Figure 1). Ten percent of net primary production is subtracted annually as a reproductive cost. To ensure conservation in the system, this carbon is transferred to aboveground litter. The remaining carbon is added to plant mass, subtracting turnover loss and satisfying allocation rules. LPJ simulates the allometry of the average PFT individual. Four scaling rules define allocation in woody PFTs: leaf area is proportional to sapwood area (Table 5); leaf mass is proportional to root mass, with greater allocation to roots as water stress increases (Table 5); height is an allometric function of stem diameter; and crown area is an allometric function of stem diameter. In contrast to LPJ, which calculates a leaf-to-root ratio from the ratio of soil water supply to potential demand, we calculate this from the ratio of gross primary production to potential production assuming unlimited soil water. For herbaceous plants, we removed the dependence of leaf-to-root ratio on water stress and instead used a fixed ratio of 0.75 (discussed further in results).

**Mortality**

Mortality occurs annually and transfers carbon to litter (Figure 1). Herbaceous PFTs complete their life cycle in one year, so mortality is not explicitly represented. Among woody PFTs, mortality reduces the PFT population density. All individuals die if the average individual has a negative biomass increment. Otherwise, mortality is inversely related to growth efficiency, constrained to a maximum mortality rate (Table 5). This is 1% per year except for boreal deciduous trees, which have a maximum mortality of 3% per year to reflect their short longevity (discussed further in results).

A bioclimatic rule designed to mimic tolerance of cold temperatures kills established PFTs when a 20-year running mean of the minimum monthly temperature is less than some threshold (Table 1). The 20-year period prevents large year-to-year fluctuation in community composition. In addition, heat stress,
defined by the annual degree-days above 23°C for boreal trees (Table 1), kills some percent of the population.

**Aboveground competition**

Competition for light also causes mortality. Although each PFT patch is spatially independent, competition for light occurs based on the PFT’s foliage projective cover (FPC), which is also the fractional extent of the patch in the grid cell. This is the average individual’s foliage projective cover multiplied by its crown area (m^2) and population density (m^2), i.e.,

$$FPC_{gridcell} = FPC_{individual} \times \text{crown area} \times \text{density}. $$

The foliage projective cover of an individual is

$$FPC_{individual} = 1 - e^{-0.5 \text{ leaf area index}}$$

where leaf area index is derived from leaf mass (g C), specific leaf area (m^2 g C^{-1}, Table 5), and crown area (m^2) as

$$\text{leaf area index} = \left(\frac{\text{leaf mass} \times \text{specific leaf area}}{\text{crown area}}\right)^{1/2}.$$

If $FPC_{gridcell}$, summed over all PFTs, exceeds one, woody PFTs are favored over herbaceous PFTs as a result of their dominant position in the canopy. If the sum of $FPC_{gridcell}$ for woody PFTs exceeds 0.95, the density of individuals is reduced in a self-thinning like process, favoring those PFTs with a higher annual increment in foliage projected cover.

**Establishment**

Establishment of new individuals occurs annually (Figure 1). Establishment of woody PFTs occurs through an increase in population density. A maximum rate of establishment (Table 5) is scaled by the fraction of the grid cell not covered by woody vegetation, limiting establishment to gaps in the canopy. This establishment is divided equally among regenerating PFTs. Saplings of woody PFTs are assigned an initial leaf area index, from which carbon pools are derived. This carbon is added to the average individual so that no age- or size-classes are recognized. Establishment of herbaceous PFTs occurs as an increase in
leaf and root carbon. A maximum rate of increase in these pools is scaled by the non-vegetated portion of the grid cell and divided equally among herbaceous PFTs.

Several bioclimatic rules constrain regeneration (Table 1). Only PFTs that survive in the current climate can regenerate. No establishment occurs when annual precipitation is less 100 mm. This prevents regeneration in regions of severe water deficiency. Regeneration is prohibited when the 20-year running mean of the minimum monthly temperature is greater than an upper threshold, mimicking a winter chilling requirement. Growing season warmth requirements are represented by annual growing degree-days. Establishment is precluded when this is less than a PFT-specific limit.

Fire

Occurrence of fire is calculated annually (Figure 1) based on fuel load and the annual sum of daily fire probability (Thonicke et al. 2001). The probability of occurrence of at least one fire in a day is

\[ p = e^{-\pi (m/m_e)^2} \]

where \( m \) is fuel (soil) moisture and \( m_e \) is a threshold moisture. The threshold moisture above which fire does not spread can vary among PFTs, reflecting different fuel flammability, but is currently 30% of available water holding capacity (Table 5). A minimum fuel load of 200 g C m\(^{-2}\) is required for combustion. Annual fire season length, defined as the annual sum of the daily probability of fire, determines the fractional area burnt. The percent of the PFT population killed within the fractional area burnt depends on fire resistance (Table 5). Tropical deciduous and temperate broadleaf evergreen trees have high fire resistance, reflecting adaptation to recurring fires in dry tropical and subtropical climates. Herbaceous PFTs complete their life cycle in one year, so mortality by fire is not represented. Carbon of killed individuals is released to the atmosphere. Aboveground litter in the fractional area burnt is released to the atmosphere.

Phenology

Leaf area index is updated daily to not exceed a maximum value set by the annual vegetation dynamics (Figure 1). Woody PFTs utilize evergreen, summergreen, or raingreen phenologies (Table 5). Grasses have no assigned phenology. We did not use the leaf phenology of LPJ because the summergreen
phenology requires knowledge of air temperature for a full year to determine the warmest and coldest months in that year. This information is not available in a climate model.

Instead, we used phenologies similar to IBIS (Kucharik et al. 2000). Summergreen trees grow leaves when the accumulated growing degree-days above 0°C exceed 100. Leaf emergence occurs over a period equal to 50 degree-days. Leaf senescence occurs when the 10-day running mean air temperature drops below a threshold. This threshold is the larger of two temperatures: 0°C or 5°C warmer than the coldest 10-day running mean temperature in the year (in contrast IBIS uses 5°C warmer than the coldest monthly temperature). Leaf drop occurs over 15 days. Raingreen trees always maintain a small residual leaf area and grow new leaves when the 10-day running mean net photosynthesis is positive. Negative net photosynthesis initiates leaf drop. Leaf emergence and senescence occurs over 15 days. Similar to LPJ, we enforce a minimum 6-month leaf-off period for raingreen PFTs. Grasses can follow a summergreen, raingreen, or evergreen phenology. Grasses drop their leaves over 5 days when the 10-day running mean air temperature is below freezing or if the 10-day running mean net photosynthesis is negative. They green-up over 5 days when temperature is above freezing or net photosynthesis is positive.

Model simulations

The LSM-DGVM model was configured for a global 3° by 3° spatial grid. The necessary soil texture and other surface data were as in Bonan et al. (2002) for the standard NCAR LSM. The model was integrated for 200 years from an initial condition of bare ground, driven with atmospheric data from the period 1979 to 1998 (Bonan et al. 2002). The 20-year data was repeated 10 times for the full length of the simulation. LPJ simulations are also shown, forced with the same atmospheric data.
Results and discussion

Global vegetation

The global distribution of PFTs, as a percent of land area, is quite similar to that simulated by LPJ (Figure 2, Figure 3). In both models, grasses initially dominate and decline as trees grow. Peak dominance of C3 and C4 grasses is similar in both models, but C3 grasses decline slower in LSM-DGVM. Abundance at 200 years (C3, 10%; C4, <5%) is similar in both models. Tropical trees attain equilibrium rapidly in both models (about 50 years), though broadleaf deciduous trees grow slower in LSM-DGVM. Equilibrium values of 10-13% broadleaf evergreen and about 5% broadleaf deciduous trees are similar in both models. In both models, temperate forests are dominated by broadleaf deciduous trees (about 8%); broadleaf and needleleaf evergreen trees each cover less than 5% of land. The greatest difference between the models is their simulation of boreal forests. Boreal deciduous and needleleaf evergreen trees each cover about 10% of land at equilibrium in LPJ. In LSM-DGVM, deciduous trees initially dominate, followed by needleleaf evergreen trees.

Figure 4 and Figure 5 illustrate global biogeography at 50, 100, 150, and 200 years for LSM-DGVM. Grasses initially dominate in the absence of trees and die back with the establishment of forests. The grasslands of North America, South America, Africa, and central Asia are maintained throughout the simulation. Grass cover is likely lower than observations. Other dynamic global vegetation models have higher coverage in the U.S. Great Plains, southern South America, Africa, and India (Kucharik et al. 2000; Cramer et al. 2001). Tropical evergreen trees establish early, attaining greater than 90% cover by 50 years, and change little over time. Temperate summergreen trees also establish rapidly in eastern U.S. and Europe; their biogeography changes relatively little over the last 100 years. Boreal forests establish slowly. After 100 years, needleleaf evergreen trees comprise less than 40% of area in Alaska, northern Canada, and northern Russia. By 150 years, they comprise more than 50% of the area of many grid cells, and attain greater dominance by year 200.

The biogeography of trees after 200 years compares favorably with their fractional coverage derived from satellite observations (Figure 6). Broadleaf evergreen trees are more extensive in southern Brazil, India, and southeast Asia than in the observations. These are regions of high crop cover (Figure 6), which could account for the discrepancy. In Africa, broadleaf evergreen trees compare favorably with
observations in the tropical rainforest, but are overestimated in the savannas to the north and south. Needleleaf evergreen trees have highest abundance in northern Canada and Russia as in the observations, though they extend too far north in Canada. Summerrgreen deciduous trees attain highest dominance in eastern U.S., Europe, and parts of Southeast Asia. Observations show much less tree cover in these regions than in the simulations, but this is likely due to high crop cover.

When aggregated to biomes, the simulated biogeography compares well with natural vegetation (Figure 7, Table 6). One prominent deficiency is a greater extent of tropical forests at the expense of savanna. Another prominent deficiency is the absence of grasses in western U.S., parts of central Asia, southern Africa, and much of Australia, where the natural vegetation is desert scrub. The LSM-DGVM biogeography also compares well with that simulated by 6 dynamic global vegetation models (Cramer et al. 2001). Of these models, 3 have high abundance of grasses in the regions where LSM-DGVM has low grass cover, but two (IBIS and TRIFFID) also have low grass abundance in western U.S., parts of central Asia, southern Africa, and much of Australia.

Global net primary production is lower in LSM-DGVM than in LPJ (Figure 8). Equilibrium values of 65 Pg C yr⁻¹ (averaged over the last 20 years) are comparable to a range of 44-66 Pg C yr⁻¹ (mean±SD, 54±8 Pg C yr⁻¹) found in a comparison of 14 net primary production models (Cramer et al. 1999) and 45-60 Pg C yr⁻¹ found in a comparison of 6 dynamic global vegetation models (Cramer et al. 2001). Net primary production for LPJ (78 Pg C yr⁻¹ averaged over the last 20 years) is higher than reported elsewhere (Cramer et al. 2001; McGuire et al. 2001). This is likely because previous studies spun-up the model with pre-industrial atmospheric CO₂ and climate and then allowed transient dynamics from the mid-1800s to late-1900s whereas our simulations used present-day climate and CO₂. Biome average net primary production compares favorably with simulated values for IBIS and with observations (Table 6). The one prominent deficiency is the low productivity of grasslands, which is common also to IBIS. This low productivity in combination with sparse grasslands led us to remove the soil water dependence of leaf-to-root ratio.

Total plant carbon has not attained equilibrium after 200 years in either model (Figure 9). Leaf and root carbon reach equilibrium quickly. These two pools are relatively similar in LSM-DGVM, but LPJ has more root mass than foliage. Stem sapwood mass reaches equilibrium after about 160 years, with slightly
higher mass in LSM-DGVM than in LPJ. Heartwood is still accumulating after 200 years in both models, with LSM-DGVM having higher mass.

The evergreen, raingreen, and sumergreen phenologies are evident in simulated monthly leaf area index (Figure 10). Tropical forests along the equator have high leaf area index throughout the year. Dry forests to the north and south have highest leaf area during the rainy season. Temperate, boreal, and arctic regions have sumergreen phenology. Summer leaf area index of 3-8 m² m⁻² throughout much of North America, Europe, and Russia is consistent with satellite-derived leaf area (Figure 11). Forested leaf area index compares favorably with observations of 2-6 m² m⁻² in boreal forests and 1-8 m² m⁻² in temperate forests (Kucharik et al. 2000). However, simulated leaf area index of 9-10 m² m⁻² throughout much of the tropics is greater than satellite observations (Figure 11) and values of 5-8 m² m⁻² reported for tropical forests (Kucharik et al. 2000).

Changes in biogeography and vegetation structure over time alter albedo and surface energy fluxes. Figure 12 illustrates the nature of these biogeophysical feedbacks, showing planetary surface albedo over the simulation. Planetary surface albedo declines over time from a high of about 0.245 with initial grass dominance to a low of almost 0.2 as trees dominate the planet.

**Vegetation dynamics**

Simulated vegetation dynamics is illustrated for five individual grid cells where the natural vegetation is tundra, boreal forest, temperate deciduous forest, tropical rainforest, and savanna. The recovery of vegetation from bare ground is documented and the simulated succession is compared to generalized patterns of succession for that biome. Emphasis is placed on PFT composition, vegetation structure, and net primary production.

The dynamics of tundra vegetation is limited in that the model represents tundra as herbaceous plants without shrubs or mosses. Thus, the model cannot represent succession in shrub tundra along riverbanks (Bliss & Cantlon 1957; Bliss 2000). Elsewhere, however, plant succession in the Arctic is generally not characterized by the classic successional pattern of species replacement (Bliss 2000). In the low Arctic, vegetation recovery following disturbance is relatively rapid over 25 years or less (Bliss 2000). Studies of tussock tundra have found plant cover, production, or biomass nearly recovered to pre-
disturbance levels within 2 years (Wein & Bliss 1973), 5-6 years (Racine et al. 1987), 5-10 years (Chapin & Chapin 1980), and 13 years (Fetcher et al. 1984). Recovery of vascular plants occurs over a 50-100 year period in the high Arctic (Bliss 2000).

The model captures this recovery of vegetation fairly well (Figure 13). Within less than 25 years, plant cover reaches an equilibrium value of about 80%. Net primary production and plant mass recover more slowly, attaining pre-disturbance levels after about 40 years. At equilibrium, aboveground plant mass (Table 7) is comparable to observed values of 42-210 g C m^{-2} for wet sedge and tussock tundra (Bliss 2000, assuming a carbon content of 50% in dry biomass). The simulated root mass gives a lower root:shoot ratio (1.3:1) than observed values of 2:1 or 3:1 (Bliss 2000). The simulated tundra is more productive than reported values of 75-100 g C m^{-2} yr^{-1} (Bliss 2000). For comparison, simulations with LPJ for the same site (not shown) allow trees to exist, suggesting shrub or forest tundra.

In the boreal forest of interior Alaska and Canada, forest communities are a successional mosaic of quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) B.S.P.) that reflects recovery from recurring fires (Van Cleve et al. 1983a,b, 1986, 1991; Bonan 1989, 1990a,b; Bonan & Van Cleve 1992). Post-fire recovery of warm, upland sites in interior Alaska illustrates the classic shifting dominance from broadleaf deciduous trees (aspen, birch) to needleleaf evergreen trees (white spruce) over time. Shrubs and tree saplings dominate for about 25 years following fire, when the saplings grow into a dense stand of deciduous trees. These deciduous trees dominate for the next 50 years, though white spruce seedlings and saplings grow in the understory. After about 100 years, the short-lived, fast-growing deciduous trees begin to die and white spruce grows into the canopy.

The model reproduces this succession (Figure 14). Grasses initially dominate in terms of percent cover. Peak dominance is achieved at 13 years, followed by a rapid decline in grasses and increase in deciduous trees. Deciduous trees attain greatest coverage at 82 years. Thereafter, they decline in areal extent. The conversion from primarily deciduous to evergreen dominated forest occurs at 145 years, after which evergreen trees increase to 76% of the area and deciduous trees decline to 15%. Grasses maintain 9% coverage.
The succession simulated by LSM-DGVM is markedly different from that of LPJ (Figure 15). LPJ has similar initial dominance by grasses, but needleleaf evergreen trees always dominate over deciduous trees. This is related to the higher net primary production of needleleaf evergreen trees compared to deciduous trees in LPJ (Figure 15). In contrast, LSM-DGVM has lower net primary production for needleleaf evergreen trees than for deciduous trees. With LSM-DGVM, dominance by needleleaf evergreen trees is achieved using a maximum mortality rate for boreal deciduous trees of 3% per year versus 1% per year for needleleaf evergreen trees. This reflects the short life-span of deciduous trees, but is in contrast to LPJ, where a constant 1% per year is used for all PFTs. Figure 16 illustrates the effect of increasing mortality on the simulated succession. With the maximum mortality of boreal deciduous trees increased from 1% per year to 2% and 4%, deciduous trees decline in the later stages of succession.

Equilibrium is not attained until between 800-1000 years, although the time to reach equilibrium varies among model variables (Figure 14, Table 7). Net primary production reaches constant values by 250-300 years. Foliage and root mass attain equilibrium by about 100 years. Stem sapwood and leaf area attain near constant values by about 500 years. The composition of the forest at 250 years (66% evergreen, 28% deciduous, 5% grass) is close to equilibrium, though this is not attained until about 800 years. The largest trend is in heartwood mass, which accumulates carbon throughout the simulation.

Year 250 is significant because recurring fires preclude much older stands in nature. The simulated net primary production at this time (386 g C m$^{-2}$ yr$^{-1}$) is similar to observations. Van Cleve et al. (1983b) found that aboveground net primary production for white spruce stands near Fairbanks, Alaska, ranges from 119-270 g C m$^{-2}$ yr$^{-1}$ (assuming a carbon content of 50% in dry biomass) with a mean of 183 g C m$^{-2}$ yr$^{-1}$. Ruess et al. (1996) subsequently reported a similar mean for floodplain and upland white spruce (183 and 227 g C m$^{-2}$ yr$^{-1}$, respectively) and found that fine root production is 49% of total tree production. This gives average estimates of total net primary production of 359 g C m$^{-2}$ yr$^{-1}$ for the Van Cleve et al. (1983b) study and 359 and 445 g C m$^{-2}$ yr$^{-1}$ for the Ruess et al. (1996) study. In northern Canada, Gower et al. (1997) and Steele et al. (1997) estimated total net primary production of two needleleaf evergreen forests to be 222 and 286 g C m$^{-2}$ yr$^{-1}$. Simulated foliage mass (195 g C m$^{-2}$) is on the low end of average values of 280-624 g C m$^{-2}$ reported for spruce stands in interior Alaska (Van Cleve et al. 1983b) and 103-505 g C m$^{-2}$ reported for needleleaf evergreen stands in northern Canada (Gower et al. 1997). Sapwood
and heartwood mass (4757 g C m\(^{-2}\)) is comparable to a range of 2216-7776 g C m\(^{-2}\) in interior Alaska and 3556-4924 g C m\(^{-2}\) living and standing dead wood in northern Canada (Gower et al. 1997). Fine root mass (223 g C m\(^{-2}\)) is higher than values of 110-152 g C m\(^{-2}\) in interior Alaska (Ruess et al. 1996).

The Hubbard Brook study provides a detailed description of succession in northern hardwood forests of New England (Likens et al. 1977; Bormann and Likens 1979). Marks (1974) summarized general changes in community composition following disturbance. During the first 2-3 years following clear-cutting, raspberry and blackberry (Rubus species) flourish, complete their life cycles, and then decline in importance. These are replaced by pin cherry (Prunus pensylvanica L.f.), a common early successional tree species restricted to recently disturbed forests. These trees grow fast and are short-lived. Canopy closure occurs rapidly when large amounts of buried, viable seed form dense stands. Pin cherry dominates the canopy for the next several years. After about 25 to 35 years, sugar maple (Acer saccharum Marsh.) and American beech (Fagus grandifolia Ehrh.), which are tolerant of shade and able to survive beneath the dense pin cherry canopy, become dominant. Where pin cherry is less dense, it may be co-dominant with other fast-growing species such as yellow birch (Betula alleghaniensis Britton) and quaking aspen. Birch and aspen live longer than pin cherry, establish within the first few years following disturbance, and dominate the canopy for several decades before the slower growing maple and beech trees reach canopy status. A similar succession is reported by Delcourt & Delcourt (2000), who describe mesic northern hardwood forests as dominated by quaking aspen, paper birch, and balsam poplar (Populus balsamifera L.) in the early stages of succession and by sugar maple, American beech, and yellow birch in the late stages of succession.

LSM-DGVM replicates this general pattern of succession (Figure 17). Grasses initially dominate, followed by boreal deciduous trees. These trees decline in cover and by 100 years temperate broadleaf deciduous trees dominate. Boreal needleleaf evergreen trees maintain relatively low coverage, with a peak of almost 20% early in the simulation and then declining over time. This is consistent with the observed community composition of Hubbard Brook, where sugar maple, American beech, and yellow birch are the principal tree species, with a small component of other temperate and boreal species (Bormann et al. 1970). This succession is quite different from that simulated by LPJ, which gives a primarily deciduous forest with equal amounts of boreal and temperate PFTs and a high abundance of boreal needleleaf evergreen trees.
The low abundance of boreal needleleaf evergreen trees in LSM-DGVM can be attributed to their low productivity. Boreal deciduous trees decline in abundance over time because of their high mortality. In contrast, the mortality of temperate broadleaf deciduous trees was not increased because this PFT represents a mix of species from short-lived trees to longer-lived maple and beech.

Equilibrium PFT composition, net primary production, and biomass are attained over a period of 400-600 years (Figure 17, Table 7). Total net primary production (603 g C m\(^{-2}\) yr\(^{-1}\)) is comparable to a value of 522 g C m\(^{-2}\) yr\(^{-1}\) reported by Whittaker et al. (1974). Total tree mass is 18.9 kg C m\(^{-2}\), which is comparable to estimates of 16.2-19.5 kg C m\(^{-2}\) (Bormann & Likens 1979) and 21 kg C m\(^{-2}\) for old-growth stands. Likewise, leaf area index (6 m\(^{2}\) m\(^{-2}\)) is comparable to the range of 5-7 m\(^{2}\) m\(^{-2}\) observed in older forests (Aber 1979). Net primary production, leaf area index, and foliage, root, and sapwood mass are fairly similar in both models, but LSM-DGVM has considerably higher heartwood mass than LPJ (Figure 17, Figure 18). This is because of slightly higher sapwood mass in LSM-DGVM, which then accumulates as heartwood.

LSM-DGVM simulates a tropical broadleaf evergreen forest for the grid cell located in the Amazon (Figure 19). Grasses attain peak dominance after 5 years. Tropical broadleaf evergreen trees gain dominance rapidly, achieving 81% coverage by 17 years. LPJ has similar vegetation dynamics (not shown), but maintains a lower coverage of broadleaf evergreen trees (65% of grid cell) and higher broadleaf deciduous trees (30%). The simulated forest growth is similar to that observed in tropical rainforests. Richards (1979), Ewel (1983), and Whitmore (1990) describe a succession in which weedy herbaceous plants attain rapid coverage following large-scale disturbance. This initial herbaceous stage does not last long, and pioneer trees establish early. These trees form a closed canopy within a few years, but are short-lived and are replaced by slower-growing, longer-lived species capable of reproducing in shade after about 20 years or so. The succession from pioneer to climax species is not replicated in LSM-DGVM because we allow only one tropical broadleaf evergreen PFT.

Net primary production (Table 7) is within the range of observations for tropical broadleaf evergreen forests (mean±SD 1250±900 C m\(^{-2}\) yr\(^{-1}\), Kucharik et al. 2000). Leaf area index (Table 7) is greater than values of 5-8 m\(^{2}\) m\(^{-2}\) reported for tropical forests (Kucharik et al. 2000), reflecting the generally high simulated leaf area of tropical forests (Figure 10). Total plant mass is 31084 g C m\(^{-2}\), of
which two-thirds is heartwood (Table 7). The reliability of tropical forest biomass estimates is poor, but it is likely that the simulated value is high. Schlesinger (1997) reports a mean plant mass of 15000 g C m$^{-2}$ for tropical wet forests. Brunig (1983) reports average biomass ranges from 15000-32500 g C m$^{-2}$ (assuming 50% carbon in dry biomass) in tropical rainforests. He cites a value of 19550 g C m$^{-2}$ in the Amazon, which is thought to be typical of forests in tropical America. Indeed, Golley (1983) lists values of 18800 and 21000 g C m$^{-2}$ (assuming 50% carbon in dry biomass) for two tropical forests in Panama and Brazil. LPJ simulates plant mass of about 19000 g C m$^{-2}$, with substantially less sapwood (6000 g C m$^{-2}$) and heartwood (12000 g C m$^{-2}$) than LSM-DGVM. This reflects lower net primary production (about 1300-1400 g C m$^{-2}$ yr$^{-1}$), likely due to the greater abundance of deciduous trees.

LSM-DGVM simulates a mixture of tropical broadleaf deciduous trees and C$_4$ grasses for the savanna grid cell in the African Sahel (Figure 20). Grasses initially dominate, covering close to 100% of the grid cell after 10-30 years. Thereafter, they decline in coverage and trees increase. By about 80 years, trees are more extensive than grasses. Trees continue to increase in coverage, reaching maximum extent between years 120-160. At year 164, trees decline in coverage, ranging from about 60-70% of the grid cell for the rest of the simulation, and grasses increase to about 30-40%. Leaf area index is high while grasses dominate, declines, and then increases again as trees grow (Figure 20). After year 164, leaf area index varies regularly from year-to-year with peak values of about 5 m$^2$ m$^{-2}$.

The abrupt change in PFT coverage at year 164 is triggered by a large fire that burns 18% of the grid cell (Figure 20). Prior to this, fires occur sporadically and vary in extent. After year 164, fires are much more frequent and regular. This change in fire behavior is related to changes in soil water. For the first 80 years, when grasses dominate the grid cell, the top 30 cm of soil is depleted of water each year (see annual minimum soil water, Figure 20). Fires occur each year, but large fires that burn more than 5% of the grid cell only occur in dry years. As trees begin to dominate, leaf area index increases. Maximum soil water content decreases somewhat, but more significantly the soil is not as depleted of water during the year. As the trees mature, they apparently overshoot the leaf area the site can support. Interannual variability in the prescribed 20-year precipitation cycle has relatively little effect on maximum soil water until years 156-166. As annual precipitation during this period decreases from a high of 887 mm to a low of 472 mm,
maximum soil water decreases leading to the large fire in year 164. Thereafter, lower leaf area index and a more equal distribution of trees and grasses is maintained.

The savanna simulations demonstrate the importance of fire in maintaining a high abundance of grasses. This is consistent with the ecology of savannas (Walker 1981; Scholes & Walker 1993; Sims & Risser 2000). Additionally, the availability of soil water maintains the balance between grasses and trees (Walker 1981). In LSM-DGVM this is manifested in the way in which interannual precipitation variability maintains a grass-tree mixture. Simulations that use a perpetually dry, average, or wet year give vegetation dominated by either grasses or trees depending on precipitation (Figure 21). A mixture of grasses and trees is only maintained when precipitation varies from year-to-year (Figure 20). This is consistent with coupled climate-vegetation model results showing two stable regimes (wet-forest, dry-desert) in West Africa (Wang & Eltahir 2000) and that interannual variability in precipitation contributes to the maintenance of African savanna (Zeng & Neelin 2000).
Conclusions

These results show that simple physiological and ecological assumptions can result in realistic simulation of global biogeography and net primary production. LSM-DGVM simulates biogeography and net primary production that are consistent with observations (Figure 6, Figure 7, Table 6). The dynamics of tundra (Figure 13), boreal forest (Figure 14), northern hardwood forest (Figure 17), and tropical rainforest (Figure 19) are consistent with generalized succession and post-disturbance vegetation recovery in these ecosystems. Simulations for savanna show the expected importance of fire and precipitation variability in maintaining a grass-tree mixture (Figure 20, Figure 21).

The success of the model is achieved without explicit representation of individual plants, age- or size-structure, gap dynamics, and the mosaic pattern of landscapes – principles that have dominated forest dynamics theory and models for over 25 years (Bormann & Likens 1979; Shugart 1984, 1998, 2000). Instead, each PFT patch is treated as a uniform dynamic unit. Gap dynamics is implicit. It occurs not at the scale of an individual, but rather in bulk parameterizations in which establishment is limited to openings in the canopy and in which competition for space that favors PFTs with high leaf area. Moreover, the model distinguishes processes affecting the average individual (e.g., allometry) from those affecting population density (e.g., mortality, establishment). A comparison of an individual plant model of vegetation dynamics and a modified version of LPJ shows that the LPJ approach successfully captures community composition and succession (Smith et al. 2001). However, the individual-based model performs better in mixtures of deciduous and evergreen PFTs and in areas where pronounced seasonal water stress favors grasses over trees. These differences are a result of particular processes (light competition, stress related mortality) and suggest greater attention be paid to modeling mixed PFT vegetation.

The current definition of PFTs is based on physiological and morphological traits along with climatic preferences, in a manner similar to that proposed by Running et al. (1995) and Nemani & Running (1996). The distinction between annual or perennial, evergreen or deciduous, broadleaf or needleleaf, and woody or non-woody is useful because these characteristics are observable from remote sensing and are key ecological properties determining stomatal conductance, photosynthesis, and allocation. This physiological and morphological definition of PFTs must be reconciled with an understanding of plant responses to disturbance, which is so critical to modeling vegetation dynamics. Indeed, ecologists have
long characterized plants by life-history characteristics related to disturbance: r and K strategies (MacArthur & Wilson 1967; Gadgil & Solbrig 1972); early and late succession (Bazzaz 1979; Huston & Smith 1987); exploitive and conservative (Bormann & Likens 1979); ruderal, stress tolerant, and competitive (Grime 1979, 1993); vital attributes such as method of arrival following disturbance, method of persistence during and after disturbance, and ability to establish and grow to maturity (Noble & Slayter 1980); and gap and nongap species (Shugart 1984, 1998). In many cases, morphological and physiological considerations impose correlated life-history traits. In the boreal forest succession (Figure 14), the distinction between broadleaf deciduous and needleleaf evergreen also captures important differences in longevity, which drives stand dynamics. The tropical rainforest succession (Figure 19), however, with only one broadleaf evergreen PFT, does not capture the observed succession from pioneer to climax species driven by gap dynamics (Richards 1979; Ewel 1983; Whitmore 1990).

Smith et al. (2001) used a version of LPJ in which they distinguished shade tolerant and intolerant broadleaf deciduous PFTs to simulate vegetation dynamics at several locations in Europe. The shade intolerant PFT had faster growth, shorter longevity, higher sapling establishment, and needed more light for establishment than did the shade tolerant PFT. The model reproduced the classical successional series in which herbaceous ruderal species are replaced first by fast-growing, light-demanding pioneer species that give way to shade tolerant species. Future work must determine the critical aspects of succession and plant life histories necessary to represent vegetation dynamics as a climate feedback. These feedbacks include changes in albedo, surface roughness, surface energy fluxes, and carbon storage in relation to community composition and ecosystem structure. What are the number of PFTs and their critical attributes needed to adequately represent ecological succession, biogeography, and climate feedbacks?
Acknowledgements

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References


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Table 1. Bioclimatic parameters for survival and establishment. Only PFTs that survive can establish. $T_c$, coldest minimum monthly air temperature (20-year running mean) for survival of established plants; $T_{hs}$, heat stress air temperature for survival; $T_w$, warmest minimum monthly air temperature (20-year running mean) for establishment of new plants; GDD, minimum annual growing degree-days above 5°C (20-year running mean) for establishment; $P_{min}$, minimum annual precipitation for establishment.

<table>
<thead>
<tr>
<th>Plant Functional Type</th>
<th>Survival</th>
<th>Establishment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$T_c$ (°C)</td>
<td>$T_{hs}$ (°C)</td>
</tr>
<tr>
<td><strong>Trees</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropical broadleaf evergreen tree (BET)</td>
<td>15.5</td>
<td>-</td>
</tr>
<tr>
<td>Tropical broadleaf deciduous tree (BDT)</td>
<td>15.5</td>
<td>-</td>
</tr>
<tr>
<td>Temperate needleleaf evergreen tree (NET)</td>
<td>-2.0</td>
<td>-</td>
</tr>
<tr>
<td>Temperate broadleaf evergreen tree (BET)</td>
<td>3.0</td>
<td>-</td>
</tr>
<tr>
<td>Temperate broadleaf deciduous tree (BDT)</td>
<td>-17.0</td>
<td>-</td>
</tr>
<tr>
<td>Boreal needleleaf evergreen tree (NET)</td>
<td>-32.5</td>
<td>23</td>
</tr>
<tr>
<td>Boreal deciduous</td>
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<td>23</td>
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<td>$C_4$</td>
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</tr>
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<td>$C_3$</td>
<td>-17.0</td>
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<tr>
<td>$C_3$ arctic</td>
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Table 2. Optical properties for canopy radiative transfer. See Table 1 for a definition of the plant types. Reflectance and transmittance are for visible (VIS) and near-infrared (NIR) wavebands.

<table>
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<tr>
<th>Plant Functional Type</th>
<th>Leaf Angle</th>
<th>Leaf Reflectance VIS</th>
<th>Leaf Reflectance NIR</th>
<th>Stem Reflectance VIS</th>
<th>Stem Reflectance NIR</th>
<th>Leaf Transmittance VIS</th>
<th>Leaf Transmittance NIR</th>
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<tr>
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<td>0.10</td>
<td>0.45</td>
<td>0.16</td>
<td>0.39</td>
<td>0.05</td>
<td>0.25</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Tropical BDT</td>
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<td>0.10</td>
<td>0.45</td>
<td>0.16</td>
<td>0.39</td>
<td>0.05</td>
<td>0.25</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Temperate NET</td>
<td>0.01</td>
<td>0.07</td>
<td>0.35</td>
<td>0.16</td>
<td>0.39</td>
<td>0.05</td>
<td>0.10</td>
<td>0.001</td>
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<tr>
<td>Temperate BET</td>
<td>0.10</td>
<td>0.10</td>
<td>0.45</td>
<td>0.16</td>
<td>0.39</td>
<td>0.05</td>
<td>0.25</td>
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<td>Temperate BDT</td>
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<td>0.10</td>
<td>0.45</td>
<td>0.16</td>
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<td>0.05</td>
<td>0.25</td>
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<tr>
<td>Boreal NET</td>
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<td>0.07</td>
<td>0.35</td>
<td>0.16</td>
<td>0.39</td>
<td>0.05</td>
<td>0.10</td>
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<td>0.25</td>
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<td>C₄</td>
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<td>0.36</td>
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<td>0.220</td>
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<tr>
<td>C₃ arctic</td>
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<td>0.11</td>
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<td>0.36</td>
<td>0.58</td>
<td>0.07</td>
<td>0.25</td>
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Table 3. Physiological parameters for leaf photosynthesis and stomatal conductance. See Table 1 for a definition of the plant types. $V_{\text{max}25}$, maximum rate of carboxylation at 25°C; m, slope of conductance-photosynthesis relationship; $T_{\text{min}}$, lowest temperature for photosynthesis.

<table>
<thead>
<tr>
<th>Plant Functional Type</th>
<th>$V_{\text{max}25}$</th>
<th>Quantum Efficiency</th>
<th>m</th>
<th>$T_{\text{min}}$</th>
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<tr>
<td></td>
<td>($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>($\mu$mol CO$_2$ $\mu$mol photon$^{-1}$)</td>
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<tr>
<td>Woody</td>
<td></td>
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<tr>
<td>Tropical BET</td>
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<td>0.06</td>
<td>9</td>
<td>5</td>
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<td>Tropical BDT</td>
<td>40</td>
<td>0.06</td>
<td>9</td>
<td>5</td>
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<tr>
<td>Temperate NET</td>
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Table 4. PFT morphology. See Table 1 for a definition of the plant types. Roughness length and displacement height are as a fraction of canopy height. Cumulative relative root abundance at depth $z$ (cm) is $f(z) = 1 - a^z$.

<table>
<thead>
<tr>
<th>Plant Functional Type</th>
<th>Leaf Dimension (m)</th>
<th>Roughness Length</th>
<th>Displacement Height</th>
<th>Root Profile Parameter (a)</th>
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<tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropical BET</td>
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<td>0.1</td>
<td>0.7</td>
<td>0.94</td>
</tr>
<tr>
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<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.97</td>
</tr>
<tr>
<td>Temperate NET</td>
<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.94</td>
</tr>
<tr>
<td>Temperate BET</td>
<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.94</td>
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<tr>
<td>Temperate BDT</td>
<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.94</td>
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<tr>
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<td>0.1</td>
<td>0.7</td>
<td>0.94</td>
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<tr>
<td>Boreal deciduous</td>
<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.94</td>
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<tr>
<td><strong>Grasses</strong></td>
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</tr>
<tr>
<td>C$_4$</td>
<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.97</td>
</tr>
<tr>
<td>C$_3$</td>
<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.97</td>
</tr>
<tr>
<td>C$_3$ arctic</td>
<td>0.04</td>
<td>0.1</td>
<td>0.7</td>
<td>0.94</td>
</tr>
</tbody>
</table>
Table 5. Parameters for vegetation dynamics. See Table 1 for a definition of the plant types. Phenology denotes evergreen (E), raingreen (R), or summergreen (S) leaf phenology. Leaf longevity is used only to calculate specific leaf area (cm² g C⁻¹ in parentheses). Fuel moisture is the fraction of soil water holding capacity above which fire does not spread. Resistance is the fraction of individuals exposed to fire that survive.

<table>
<thead>
<tr>
<th>Plant Functional Type</th>
<th>Phenology</th>
<th>Leaf Longevity</th>
<th>Leaf-to-Sapwood Area (m² cm⁻²)</th>
<th>Leaf-to-Root Ratio</th>
<th>Turnover (years)</th>
<th>C:N Leaf</th>
<th>C:N Stem</th>
<th>C:N Root</th>
<th>Maximum Mortality (% yr⁻¹)</th>
<th>Respiration Acclimation Factor</th>
<th>Fire Resistance (individuals m⁻² yr⁻¹)</th>
<th>Fuel Moisture Resistance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trees</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Tropical BET</td>
<td>E</td>
<td>2.0 (217)</td>
<td>0.8</td>
<td>1.00</td>
<td>2</td>
<td>20</td>
<td>2</td>
<td>1</td>
<td>0.5</td>
<td>29</td>
<td>330</td>
<td>29</td>
</tr>
<tr>
<td>Tropical BDT</td>
<td>R</td>
<td>0.5 (411)</td>
<td>0.8</td>
<td>1.00</td>
<td>1</td>
<td>20</td>
<td>1</td>
<td>1</td>
<td>0.5</td>
<td>29</td>
<td>330</td>
<td>29</td>
</tr>
<tr>
<td>Temperate NET</td>
<td>E</td>
<td>2.0 (217)</td>
<td>0.8</td>
<td>1.00</td>
<td>2</td>
<td>20</td>
<td>2</td>
<td>1</td>
<td>1.2</td>
<td>29</td>
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<td>29</td>
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<tr>
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<td>E</td>
<td>1.0 (299)</td>
<td>0.8</td>
<td>1.00</td>
<td>1</td>
<td>20</td>
<td>1</td>
<td>1</td>
<td>1.2</td>
<td>29</td>
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<td>29</td>
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<tr>
<td>Temperate BDT</td>
<td>S</td>
<td>0.5 (411)</td>
<td>0.8</td>
<td>1.00</td>
<td>1</td>
<td>20</td>
<td>1</td>
<td>1</td>
<td>1.2</td>
<td>29</td>
<td>330</td>
<td>29</td>
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<tr>
<td>Boreal NET</td>
<td>E</td>
<td>2.0 (217)</td>
<td>0.8</td>
<td>1.00</td>
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<td>20</td>
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<td>1</td>
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<td>29</td>
</tr>
<tr>
<td>Boreal deciduous</td>
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<td>0.5 (411)</td>
<td>0.8</td>
<td>1.00</td>
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<td>1</td>
<td>3</td>
<td>0.6</td>
<td>29</td>
<td>330</td>
<td>29</td>
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<tr>
<td>Grasses</td>
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<tr>
<td>C₄</td>
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<td>1.2</td>
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<tr>
<td>C₃</td>
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<td>1.0 (299)</td>
<td>-</td>
<td>0.75</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1.2</td>
<td>29</td>
<td>-</td>
</tr>
<tr>
<td>C₃ arctic</td>
<td></td>
<td>-</td>
<td>1.0 (299)</td>
<td>-</td>
<td>0.75</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1.2</td>
<td>29</td>
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</table>
Table 6. Simulated biogeography and net primary production (NPP) for LSM-DGVM compared to observations and that simulated by IBIS (Kucharik et al. 2000). Vegetation type is defined by dominant PFT area in LSM-DGVM. NPP observations are mean ± standard deviation (Kucharik et al. 2000). Observed biogeography is from Ramankutty & Foley (1999).

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>LSM-DGVM</th>
<th>IBIS</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area</td>
<td>NPP (g C m⁻² yr⁻¹)</td>
<td>Area</td>
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<tr>
<td>Tropical broadleaf evergreen forest</td>
<td>21.0</td>
<td>1278</td>
<td>19.3</td>
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<tr>
<td>Tropical broadleaf deciduous forest</td>
<td>9.4</td>
<td>886</td>
<td>7.7</td>
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<tr>
<td>Temperate needleleaf evergreen forest</td>
<td>1.3</td>
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<td>3.3</td>
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<tr>
<td>Temperate broadleaf evergreen forest</td>
<td>6.0</td>
<td>821</td>
<td>7.2</td>
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<tr>
<td>Temperate broadleaf deciduous forest</td>
<td>12.6</td>
<td>561</td>
<td>9.7</td>
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<tr>
<td>Boreal needleleaf evergreen forest</td>
<td>10.6</td>
<td>352</td>
<td>14.5</td>
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<tr>
<td>Boreal deciduous forest</td>
<td>2.4</td>
<td>362</td>
<td>6.8</td>
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<tr>
<td>Temperate/boreal mixed forest</td>
<td>11.4</td>
<td>483</td>
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<tr>
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<td>4.7</td>
<td>544</td>
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<tr>
<td>Grassland</td>
<td>18.1</td>
<td>175</td>
<td>21.2</td>
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<tr>
<td>Tundra</td>
<td>9.3</td>
<td>159</td>
<td>6.2</td>
</tr>
</tbody>
</table>
Table 7. Biomass, leaf area index, net primary production (NPP), heterotrophic respiration ($R_h$), and net ecosystem production ($NEP=NPP-R_h$) simulated by LSM-DGVM for tundra, boreal forest, northern hardwood forest, and tropical rainforest ecosystems. Data are averaged over the last 20 years of simulations for individual grid cells shown in Figure 13, Figure 14, Figure 17, and Figure 19.

<table>
<thead>
<tr>
<th></th>
<th>Tundra</th>
<th>Boreal Forest</th>
<th>Northern Hardwood Forest</th>
<th>Tropical Rainforest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g C m$^{-2}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Foliage</td>
<td>112</td>
<td>182</td>
<td>152</td>
<td>667</td>
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<tr>
<td>Sapwood</td>
<td>0</td>
<td>1445</td>
<td>3084</td>
<td>8619</td>
</tr>
<tr>
<td>Heartwood</td>
<td>0</td>
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<td>15478</td>
<td>21124</td>
</tr>
<tr>
<td>Root</td>
<td>150</td>
<td>209</td>
<td>157</td>
<td>674</td>
</tr>
<tr>
<td>Leaf area index (m$^2$ m$^{-2}$)</td>
<td>3.4</td>
<td>3.3</td>
<td>5.9</td>
<td>14.7</td>
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<tr>
<td>NPP (g C m$^{-2}$ yr$^{-1}$)</td>
<td>208</td>
<td>368</td>
<td>603</td>
<td>1672</td>
</tr>
<tr>
<td>$R_h$ (g C m$^{-2}$ yr$^{-1}$)</td>
<td>168</td>
<td>356</td>
<td>585</td>
<td>1618</td>
</tr>
<tr>
<td>NEP (g C m$^{-2}$ yr$^{-1}$)</td>
<td>40</td>
<td>12</td>
<td>18</td>
<td>54</td>
</tr>
</tbody>
</table>
Figure Legends

Figure 1. Components of the LSM-DGVM model showing the coupling between fast processes such as energy exchange, photosynthesis, and respiration and slower processes such as tissue turnover, mortality, establishment, and disturbance. The model is forced with atmospheric temperature (T), winds (u,v), humidity (q), precipitation (P), and incoming solar ($S\downarrow$) and longwave ($L\downarrow$) radiation. It returns to the atmosphere latent heat ($\lambda E$), sensible heat (H), surface stresses ($\tau_x$, $\tau_y$), reflected solar radiation ($S\uparrow$), and emitted longwave radiation ($L\uparrow$). When the carbon cycle is included, CO$_2$ is also exchanged.

Figure 2. Global distribution, as a percent of land area including glaciers, of boreal, temperate, tropical, and grass PFTs simulated by LSM-DGVM over 200 years from initially unvegetated land.

Figure 3. Global distribution, as a percent of land area including glaciers, of boreal, temperate, tropical, and grass PFTs simulated by LPJ over 200 years from initially unvegetated land.

Figure 4. Geographic distribution of PFTs, as a percent of grid cell area, simulated by LSM-DGVM at 50 years (left) and 100 years (right).

Figure 5. Geographic distribution of PFTs, as a percent of grid cell area, simulated by LSM-DGVM at 150 years (left) and 200 years (right).

Figure 6. Observed (left) and LSM-DGVM simulated (right) geographic distribution of woody PFTs, as a percent of grid cell area, at 200 years. Observations are from Bonan et al. (2002).

Figure 7. LSM-DGVM simulated biogeography (top) compared to Ramankutty & Foley’s (1999) potential natural vegetation (bottom). Simulated biome type is defined by dominant PFT area.

Figure 8. Global annual net primary production simulated by LSM-DGVM and LPJ over 200 years. 1 Pg is $10^{15}$ g.

Figure 9. Global plant carbon simulated by LSM-DGVM (top) and LPJ (bottom) over 200 years. 1 Pg is $10^{15}$ g.
Figure 10. Monthly leaf area index simulated by LSM-DGVM at 200 years.

Figure 11. Satellite-derived leaf area index for January (left) and July (right) for broadleaf evergreen, needleleaf evergreen, broadleaf deciduous, and needleleaf deciduous trees (Bonan et al. 2002).

Figure 12. Annual average surface albedo over ice-free land during the 200 year LSM-DGVM simulation.

Figure 13. LSM-DGVM vegetation dynamics over 200 years from initially bare ground for a grid cell in the Canadian Arctic (65.5°N, 105.5°W). Percent cover is the annual extent of PFTs in the grid cell. Carbon fluxes and biomass are 20-year averages. Carbon fluxes are shown for net primary production (NPP), heterotrophic respiration ($R_h$), and net ecosystem production (NEP=NPP-$R_h$). Leaf area index is the maximum attained each year.

Figure 14. LSM-DGVM vegetation dynamics over 1000 years from initially bare ground for a grid cell in the Canadian boreal forest (60.5°N, 105.5°W). Percent cover is the annual extent of PFTs in the grid cell. Carbon fluxes and biomass are 20-year averages. Carbon fluxes are shown for net primary production (NPP), heterotrophic respiration ($R_h$), and net ecosystem production (NEP=NPP-$R_h$). Leaf area index is the maximum attained each year.

Figure 15. Boreal forest dynamics over 200 years simulated by LSM-DGVM (left) and LPJ (right). The top panels show percent cover of PFTs in the grid cell. The bottom panels show the annual net primary production of tree PFTs per unit patch area.

Figure 16. Boreal forest dynamics over 200 years simulated by LSM-DGVM with the maximum mortality rate of boreal deciduous trees increased to 2% per year (top) and 4% per year (bottom).

Figure 17. LSM-DGVM vegetation dynamics over 600 years from initially bare ground for a grid cell in the northern hardwood forest of Northeast U.S. (42.0°N, 74.0°W). Percent cover is the annual extent of PFTs in the grid cell. Carbon fluxes and biomass are 20-year averages. Carbon fluxes are shown for net primary production (NPP), heterotrophic respiration ($R_h$), and net ecosystem production (NEP=NPP-$R_h$). Leaf area index is the maximum attained each year.
Figure 18. As in Figure 17, but for LPJ.

Figure 19. LSM-DGVM vegetation dynamics over 400 years from initially bare ground for a grid cell in the Amazon (5.0°S, 60.0°W). Percent cover is the annual extent of PFTs in the grid cell. Carbon fluxes and biomass are 20-year averages. Carbon fluxes are shown for net primary production (NPP), heterotrophic respiration ($R_h$), and net ecosystem production (NEP=NPP-$R_h$). Leaf area index is the maximum attained each year.

Figure 20. LSM-DGVM vegetation dynamics over 300 years from initially bare ground for a grid cell in African savanna (13.5°N, 7.5°W). Percent cover is the annual extent of PFTs in the grid cell. Leaf area index is the maximum attained each year. Annual precipitation, soil water in the top 30 cm (as a percent of water holding capacity), and percent of the grid cell burned annually are also shown.

Figure 21. Annual percent cover of PFTs for the savanna grid cell simulated by LSM-DGVM using atmospheric data for dry, average, and wet years. Dry year: 1984 (annual precipitation 472 mm). Average year: 1986 (annual precipitation 624 mm). Wet year: 1994 (annual precipitation 887 mm). The average annual precipitation in the 20 year atmospheric forcing dataset is 625 mm.