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Simulating boreal forest dynamics from perspectives of ecophysiology, resource availability, and climate change

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Abstract Boreal forests are under strong influences from climate change, and alterations in forest dynamics will have significant impacts on global climate-biosphere feedback as well as local to regional conservation and resource management. To understand the mechanisms of forest dynamics and to assess the fate of boreal forests, simulation studies should be based on plant ecophysiological responses onto environmental conditions. In central Canadian boreal forests, local geomorphology created by past glacial activities often generates a mosaic of very distinctive forest types. On sandy hilltop of a glacial till, due to limitations in moisture availability and short fire return intervals, drought-tolerant and fire-adapted jack pine usually becomes the dominant species. On mesic and nutrient-rich slopes, fast-growing and resource-demanding trembling aspen forms mixed forests with coniferous species. In bottomland, black spruce, slowly growing but tolerant species, is often the only species that can survive to the adult stage. These three very distinctive forest types often occur within a scale of 10 m. Simulation models of boreal forests should be able to reproduce this heterogeneity in forest structure and composition as an emergent property of plant ecophysiological responses to varying environmental properties. In this study, a process-based forest dynamics model, ecosystem demography model version 1.0, is used to mechanically reproduce the landscape heterogeneity due

to edaphic variations. First, boreal tree species of northern Manitoba, Canada, are parameterized according to field observations, and, to explicitly capture interactions among tree saplings, allometric equations based on diameter at height of 0.15 m, instead of the conventional breast height of 1.37 m, is parameterized. Then, soil moisture regime and nutrient concentrations are statistically incorporated from a dataset. The resultant simulation successfully reproduces the distinctive forest dynamics influenced by the edaphic heterogeneity. The sequences of succession and the trajectories of forest development are generally consistent with the field observations. The differences in resource availability are the essential control on equilibrium values of total forest leaf area index. Next, to show the effect of anthropogenic atmospheric changes, changes in temperature and CO₂ concentrations are studied by a set of factorial experiments. The magnitude of CO₂ fertilization is largely affected by soil fertility. The temperature rise will increase the length of growing season, but can have a negative impact on forest growth by increasing aridity and autotrophic respiration. Overall, the boreal forest responses to climate change are complex due to the inherent edaphic variations and ecophysiological responses.

Keywords Boreal forest · Black spruce (*Picea mariana*) · Simulation modeling · Forest dynamics · Ecophysiology · Heterogeneity

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Introduction

In a large extent of boreal region, past glacial activities shaped the terrain with unique geomorphological features such as glacial tills, and boreal species compete on various niches created by the geomorphology (Brubaker 1975; Host and Pregitzer 1992; Mann et al. 1995). The variation in environmental conditions—availabilities of water and nutrients—controls forest species composition, biomass, succession, and frequency

of stand-replacing disturbance (Whittaker and Niering 1975; Chipman and Johnson 2002). For example, on top of a sandy glacial till, jack pine (JP) (*Pinus banksiana* Lamb.), a drought-tolerant and fire-adapted species, often forms even-aged, monoculture stands after disturbance. Frequent fire periodically replaces trees and keeps the mean stand age on sandy soil young (Johnson et al. 1995; Larsen 1997). On a nutrient-rich and moist mid slope, fast-growing, resource-demanding broadleaf deciduous species such as trembling aspen (TA) (*Populus tremuloides* Michx.) form mixed forest with coniferous species. At the bottom of a glacial till, slowly growing black spruce (BS) [*Picea mariana* (Mill.) B.S.P.] is the dominant species in this nutrient-poor, often waterlogged environment.

Ongoing climate change is altering averages and seasonality of temperature and precipitation in boreal regions (Serreze et al. 2000; Holland and Bitz 2003). Changes in duration and temperature of growing season, severity of winter frost, and water availability will affect forest physiology and productivity. Changes in decomposition of soil organic matter and nutrient cycling will also affect the forest dynamics (Mack et al. 2004; Ise and Moorcroft 2006). In addition to meteorological changes, increases in atmospheric CO₂ concentration have a direct fertilization effect on photosynthetic organisms and change water-use efficiency (Farquhar and Sharkey 1982; McLeod and Long 1999). Recent studies revealed that the magnitude of CO₂ fertilization differs greatly among plant types (Curtis and Wang 1998) and is affected by soil nutrient status (Oren et al. 2001). The climate change will also modify boreal fire patterns (Randerson et al. 2006) and the resultant stand age distributions.

A mechanistic forest ecosystem model based on plant physiology and physical environmental conditions is a useful tool to realistically reproduce the future dynamics of boreal ecosystems. Using a dynamic vegetation model (LPJ-GUESS), Wolf et al. (2008) simulated the forest dynamics of the Barents Region and effects of climate change. Le Goff and Sirois (2004) studied the effects of fire cycles on the two-species interaction between BS and JP in well- and poorly drained forests of Quebec. Pennanen et al. (2004) made a forest dynamics model based on details of plant life history traits and applied the model to mixed boreal forests of Quebec, without considering physical heterogeneity of the region. The previous modeling studies did not explicitly integrated effects of environmental heterogeneity, plant life traits based on ecophysiology, and climate change altogether, in a fully mechanistic manner.

In this study, we utilize and modify the ecosystem demography model version 1.0 (ED1.0; Moorcroft et al. 2001; Albani et al. 2006) to simulate boreal forest dynamics based on plant ecophysiological traits, resource availability, and climatic conditions. Three representative soil types—loam, sand, clay—are used to visualize the model's behavior, and experimental simulations using both the current and future temperature

regime and CO₂ concentrations are compared. To take an advantage of the taxonomic simplicity of boreal forest, simulated trees are parameterized to individual species—TA, JP, and BS—instead of aggregational plant functional types.

Model

The Ecosystem demography model version 1.0 (Moorcroft et al. 2001; Albani et al. 2006) is a mechanistic model of forest composition and biogeochemical dynamics (Fig. 1). The model simulates leaf-level carbon and water dynamics to tree growth, and forest dynamics such as reproduction, establishment, and mortality. Intra- and inter-specific competition for light, water, and nitrogen are controlling factors of forest dynamics. ED1.0 uses the following system of size- and age-structured partial differential equations to approximate the behavior of an individual-based, stochastic gap model:

$$\frac{\partial}{\partial t} C_i(\mathbf{z}, a, t) = -\nabla_{\mathbf{z}}[g(\mathbf{z}, \mathbf{r}, t) \cdot C_i(\mathbf{z}, a, t)] - \mu(\mathbf{z}, \mathbf{r}, t) \cdot C_i(\mathbf{z}, a, t) - \nabla_a \cdot C_i(\mathbf{z}, a, t) \quad (1)$$

$$\frac{\partial}{\partial t} p(a, t) = -\nabla_a \cdot p(a, t) - \lambda(a, t) \cdot p(a, t) \quad (2)$$

where

$$\nabla_{\mathbf{z}} = \left\{ \frac{\partial}{\partial \mathbf{z}_s}, \frac{\partial}{\partial \mathbf{z}_a} \right\}, \quad \nabla_a = \left\{ \frac{\partial}{\partial a} \right\}, \quad \int_0^{\infty} p(a, t) da = 1$$

Equation (1) describes the changing distribution of plant biomass within each grid cell, where \mathbf{z} is the array of structural (\mathbf{z}_s) and live biomass (\mathbf{z}_a) compartment sizes (kgC); $C_i(\mathbf{z}, a, t) d\mathbf{z} da$ is the biomass density (kgC m⁻²) of plants of type i and size \mathbf{z} in places disturbed a years ago at time t ; \mathbf{r} is a vector describing the resource environment (light, water, and nitrogen) experienced by an individual of size \mathbf{z} ; $g(\mathbf{z}, \mathbf{r}, t)$ is the rate at which the structural and live biomass of a plant of size \mathbf{z} in environment \mathbf{r} increase (kgC year⁻¹); and $\mu(\mathbf{z}, \mathbf{r}, t)$ is the per capita rate of tree mortality (year⁻¹). Equation (2) describes the changing dynamical distribution of landscape ages within each grid cell arising from disturbance events, where $p(a)da$ is the fraction of the grid-cell disturbed between a and $a + da$ years ago, and $\lambda(a, t)$ is the rate of disturbance (year⁻¹).

The general structure of the ED1.0 used in this study is the same as that in Moorcroft et al. (2001) and Albani et al. (2006). However, a number of modifications are made to capture the composition and structure of continental Canadian boreal ecosystems and the impact of climate change on ecosystem structure and fluxes. Details of model functions and structure such as short-term ecophysiology (e.g., photosynthesis, transpiration,

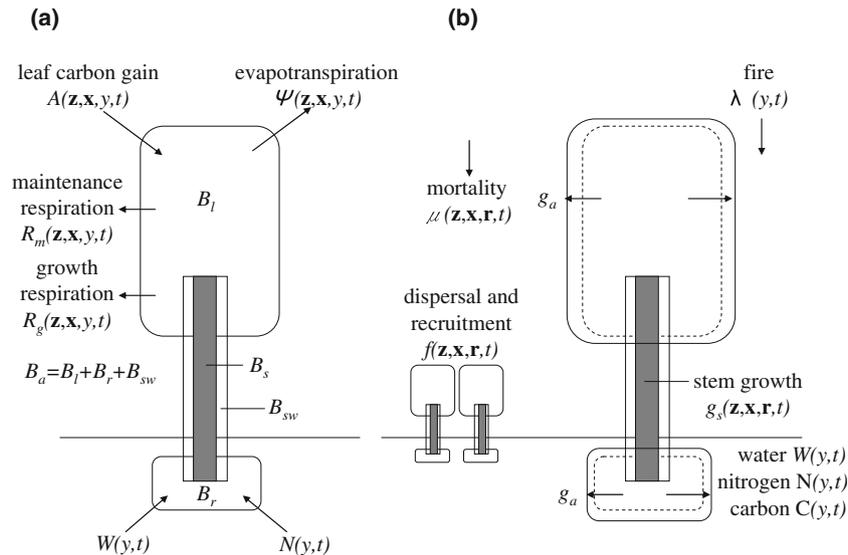


Fig. 1 **a** Individual-level fluxes of carbon, water, and nitrogen and the partitioning of carbon between active and structural tissues (B_a and B_s , respectively). **b** Summary of the processes occurring within each gap y . Each plant's structural and living tissues grow at rates g_s and g_a , respectively. Individuals die stochastically at rate μ and give birth to offspring at rate f , which are then dispersed randomly

and respiration), C partitioning for growth of metabolic and structural tissues, environmental dependency of mortality, and information on simulation runs (spatial and temporal scopes and model initialization) are described in Supplementary Information.

Boreal tree species

Three boreal tree species are parameterized from empirical data obtained around BOREAS Northern Study Area in Northern Manitoba (Sellers et al. 1995). Broadleaf deciduous trees such as TA and paper birch (*Betula papyrifera* Marsh.) are common early successional species after stand-replacing disturbance. Based on the species abundance of the study area in central Canadian boreal forest (Apps and Halliwell 1999), we use TA as the representative species of broadleaf deciduous trees. JP is another shade-intolerant species, found mainly on sandy soils. In mixed forests with deciduous species, JP often plays a role of a mid-successional species. BS is a slowly growing, shade-tolerant species found mainly in moist stands. BS is assumed to reasonably represent a closely related species, white spruce [*Picea glauca* (Moench) Voss], in this study.

Maximum photosynthetic rates

In general, shade-intolerant, early successional species have higher maximum photosynthetic rates ($Vm0$) than do shade-tolerant species (Table 1). This trade-off between faster growth and tolerance to resource limitation drives species composition changes among successional

stages. Due to the high $Vm0$ (Reich et al. 1998; Bond-Lamberty et al. 2002), TA outgrows the other species when resources (i.e., sunlight, water, and mineralized nitrogen) are abundant. As the forest canopy closes, BS, a species tolerant to resource limitations, gradually replaces TA as a late-successional species. Since JP has an intermediate $Vm0$, JP often becomes a mid-successional species in mixed forests.

Allometry

The standard practice to parameterize tree allometric relationships is to use diameter at breast height (DBH) as the predictor variable. However, the allometric equations based on DBH cannot be used in simulations of tree saplings smaller than breast height. Explicit tracking of sapling trees is beneficial for modeling of boreal forest dynamics because (1) boreal forest trees are generally smaller than temperate trees and (2) interactions among saplings are important determinants of forest dynamics of even-aged, high-density stands (Smith and Brand 1983; Greene and Johnson 1999). To model saplings, the allometric relationships of TA, JP, and BS are recalculated with a reference height of 0.15 m, instead of the standard height of 1.37 m (breast height). This re-parameterization is especially important for the future development of the model for wet BS stands, where trees are stunted and compete with shrubs. The height–diameter relationships are modified from Pacala et al. (1996):

$$H = H_{\text{ref}} + b_{1h} (1 - e^{b_{2h} D_{\text{ref}} \times 100}) \quad (3)$$

Table 1 Model parameters used in simulations of boreal forest dynamics by ED1

	<i>P. tremuloides</i>	<i>P. banksiana</i>	<i>P. mariana</i>
Leaf trait	Deciduous	Evergreen	Evergreen
$Vm0$ ($\mu\text{mol}/\text{m}^2/\text{s}$)	11.9	9.5	7.3
Specific leaf area (m^2/kgC)	28.0	10.0	13.5
Density-independent mortality	0.02	0.01	0.005
Water use efficiency	0.5	0.5	0.75
Nitrogen use efficiency	1.0	1.7	0.9
Fine root decay rate (year^{-1})	0.333	0.333	0.167
Leaf decay rate (year^{-1})	–	0.333	0.167
Number of trees in TE-23	188	595	223
B_{1h}	33.2	20.4	21.1
B_{2h}	–0.0453	–0.0547	–0.0583
a_1	0.00102	0.0116	0.0188
b_1	2.22	1.90	1.66
a_s	0.0171	0.00578	0.0137
b_s	2.71	2.95	2.65

where H is the tree's height (m), H_{ref} the reference height of 0.15 m, D_{ref} the diameter (m) at the reference height, and b_{1h} is the maximum height (m) of the species observed in the dataset. To estimate b_{2h} , a species-specific parameter, we fit Eq. (3) to the allometric dataset in the BOREAS project (TE-23; Rich and Fournier 1999) and sapling allometry. The sapling allometric relationships for TA and BS are obtained from Smith and Brand (1983). For JP, we use sapling allometric relationships of a closely related species, lodgepole pine (*Pinus contorta*) in Yellowstone National Park, WY, for biomass (Turner et al. 2004) and height (C. M. Litton, unpublished data).

To estimate D_{ref} , which is not usually measured for adult tree allometry, a simple geometric relationship of similarity of tree stem is used (Fig. 2):

$$\text{DBH} : (H - 1.37) = D_{\text{ref}} : (H - H_{\text{ref}}) \quad (4)$$

Solving Eq. (2) for D_{ref} :

$$D_{\text{ref}} = \text{DBH} \frac{H - H_{\text{ref}}}{H - 1.37} \quad (5)$$

To estimate structural biomass (B_s) and foliar biomass (B_l) of target species (kgC), the following relationships are used (Moorcroft et al. 2001):

$$B_s = a_s (D_{\text{ref}} \times 100)^{b_s} \quad (6)$$

$$B_l = a_l (D_{\text{ref}} \times 100)^{b_l} \quad (7)$$

To estimate species-specific parameters a_s , b_s , a_l , and b_l , datasets for adult trees (Rich and Fournier 1999) and saplings (Smith and Brand 1983) are combined.

Fire

Forest fire is one of the main driving forces of boreal forest dynamics, and the climate change will largely alter the frequency and severity of forest fire (Soja et al. 2007). The fire-return intervals in central Canadian boreal regions are generally short; for instance, 39 years for TA and JP forests and 78 years for BS forests in northern Alberta (Larsen 1997), and rarely more than

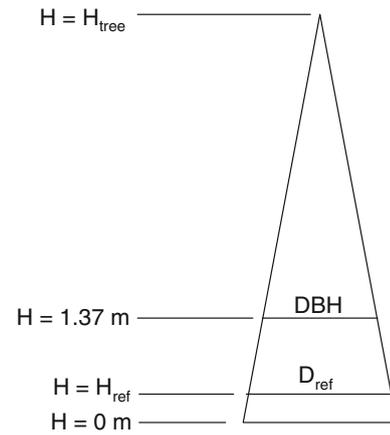


Fig. 2 Simplified stem geometry and relationship among tree height (H_{tree}), diameter at breast height (DBH), and diameter at reference height (D_{ref}). Assuming that the tree stem has a conical shape, D_{ref} can be expressed as a function of H_{tree} and DBH (see text)

5–10% of a landscape is older than 200 years (Johnson et al. 1995). To mechanistically simulate fire, at the end of the 8th month of each simulation year, λ , the probability of fire, is calculated as a function of soil moisture, by the following equation (Thonicke et al. 2001; Sato et al. 2007):

$$\lambda = s \exp\left(\frac{s-1}{0.45(s-1)^3 + 2.83(s-1)^2 + 2.96(s-1) + 1.04}\right) \quad (8)$$

where

$$s = \sum_{i=1}^{365} \exp\left(\frac{-\pi(3.33Q_i)^2}{365}\right) \quad (9)$$

where i is a day of a year starting from the first day of September and Q_i is soil water content (kg) of day i . In this large-scale simulation, λ is the fraction of the burned area in a grid cell.

Nitrogen and water use efficiencies

The three tree species have different specialized niches in both space (e.g., soil types) and time (e.g., successional stages) depending on ecophysiological traits: nitrogen use efficiency (NUE) and water use efficiency (WUE). ED1.0 calculates theoretical photosynthetic rates (A_o) for each species under given environmental conditions, without water and nitrogen limitation (Moorcroft et al. 2001). Then, degree of limitation, c^* , a composite of nitrogen limitation (c_N) and water limitation (c_W), is multiplied to A_o :

$$c^* = c_N c_W \quad (10)$$

and

$$c_N = \frac{S_N}{D_N + S_N} \quad (11)$$

$$c_W = \frac{S_W}{D_W + S_W} \quad (12)$$

where S_N , D_N , S_W , and D_W are supply and demand of nitrogen and water, respectively. D_W is calculated by ED1.0 along with photosynthetic rates (Farquhar and Sharkey 1982), and D_N is obtained from growth rate and C:N ratio of growing biomass. Amounts of nitrogen and water supplies are:

$$S_N = \text{NUE} \cdot B_r \cdot N_m \quad (13)$$

$$S_W = \text{WUE} \cdot B_r \cdot W \quad (14)$$

where NUE and WUE are species-specific parameters (Table 1), B_r is root biomass (kgC), N_m is mineralized nitrogen content (kg), and W is soil water content (kg) within rooting depth. Organic nitrogen content of each soil type is estimated from BOREAS TE-20 (Veldhuis 2000; Table 2).

Soil hydrology

In the model, the soil water budget is a balance between incoming (precipitation) and outgoing (evapotranspiration and runoff) fluxes. Groundwater runoff from the soil is modeled according to Darcy's law for porous media:

$$\frac{dW_i}{dt} = -K_i \left[\frac{dz_i}{dy} + \frac{d\psi}{dy} \right] \quad (15)$$

where W_i is volumetric water content of soil layer i , K_i is saturation hydraulic conductivity (Clapp and Hornberger 1978; Table 2) of layer i , dz_i/dy is gravitational potential energy in the vertical direction, and $d\psi/dy$ is pressure potential energy. Evaporation from soil surface is modeled by a monthly water balance model (Thorntwaite and Mather 1957; Dingman 2002). Transpirational loss of water is assigned from the photosynthesis module (Farquhar and Sharkey 1982; Moorcroft et al. 2001). The fraction of precipitation lost due to canopy interception (I) is separately modeled (Shiklomanov and Krestovsky 1988):

Table 2 Soil properties used in simulations of boreal forest dynamics by ED1

Type	Soil nitrogen content (kgN/m ²)	Saturation hydraulic conductivity (m/s)
Sand	0.03	1.76×10^{-4}
Loamy sand	0.0475	1.56×10^{-4}
Sandy loam	0.065	3.47×10^{-5}
Silt loam	0.0825	7.20×10^{-6}
Loam	0.1	6.95×10^{-6}
Sandy clay loam	0.085	6.30×10^{-6}
Silty clay loam	0.07	1.70×10^{-6}
Clay loam	0.055	2.45×10^{-6}
Sandy clay	0.04	2.17×10^{-6}
Silty clay	0.025	1.03×10^{-6}
Clay	0.01	1.28×10^{-6}
Peat	0.005	8.00×10^{-6}

Soil nitrogen content is from BOREAS TE-20 dataset (Veldhuis 2000), and saturation hydraulic conductivity is from Clapp and Hornberger (1978)

$$I = 0.05 \cdot \text{LAI} \cdot P \quad (16)$$

where LAI is leaf area index of the stand and P is monthly precipitation. Note that ED1.0 is designed to utilize monthly environmental variables (e.g., air temperature and precipitation) to reproduce relatively long-term (e.g., decades to centuries) forest dynamics. Sub-monthly variations that are not considered in this study may have effects on the simulation outputs.

Simulation under atmospheric changes

To study the changes in forest dynamics under influence of anthropogenic changes, changes in temperature, precipitation, and CO₂ concentration are applied to the model as forcings. The current climatic inputs are monthly averages of temperature and precipitation of 1961–1990 (New et al. 2000). A climatic projection for 2071–2100 by the general circulation model by Geophysical Fluid Dynamics Laboratory (GFDL R30; Delworth et al. 2002) with SRES A2 CO₂ emission scenario (IPCC 2001) is used as the future forcings of temperature, precipitation, and CO₂ concentration. In addition, to assess the future changes in forest composition, productivity, and C storage of central Canada, we make a set of regional simulations for the continental Canadian boreal forest (50–60°N and 94–104°W; 1° resolution) with both current and future atmospheric conditions. A soil texture classification dataset (Global Soil Data Task 2000) is used to represent the edaphic heterogeneity in this region.

Results

Current vegetation dynamics on loam, clay, and sand

Simulations of forest dynamics on different soil types show distinctive dynamics in species composition. Since

loam is rich in nitrogen and moisture, the most resource-demanding species, broadleaf deciduous TA, dominates the early stages of succession, over more slowly growing JP and BS (Fig. 3a). The closure of TA canopy, however, inhibits further establishment of shade-intolerant TA saplings. Less resource-intensive species, JP and BS, grow under the TA canopy and gradually replace TA through time. Without stand-replacing disturbance, BS eventually dominates the forest stand in this simulation. The fraction of BS in the total tree LAI gradually increased with the stand age (Fig. 3b). The simulated trajectory of the BS dominance followed the observed value closely.

On clay, due to its severely low nutrient availability, the growth of TA and JP are merely ephemeral, and they did not reach adult stages (Fig. 3c). The forest becomes dominated mostly by BS, the species with the highest NUE. The low nutrient availability keeps the total LAI low, compared to the forests on other soil types. Around year 30, the stand reaches equilibrium in terms of species composition and leaf area.

On sand, due to the excessive drainage, JP, the species with high WUE flourishes (Fig. 3d). The stand experiences self thinning as the trees become larger and intraspecific competition for water and nutrient becomes strong, shortly after year 50. Since JP is not very shade tolerant, regeneration from seedling establishment is limited, and the forest is eventually dominated by BS, without stand-replacing fire.

Age class distribution due to natural disturbance

The simulated fire return intervals are 59, 76, and 127 years for sand, loam, and clay, respectively. Differences in fire-return interval cause a variation in age-class distribution among sites with various drainage classes (Fig. 4). Although the water input from precipitation in the model is identical, differences in soil drainage and evapotranspiration generate the variation in the fire-return interval, leading to the distinct age-class distribution. Since the fire frequency is higher on loam than clay, the age-class distribution on loam is concentrated more on younger forests. The higher leaf area on loam due to high nutrient availability increases transpirational loss of soil water, further shortening the fire-return interval. On clay, since drainage is generally poor due to low hydraulic conductivity, fire-return interval is very long, and the age-classes distribution is flatter. Transpirational losses from the low-biomass, sparse stands on clay are lower than the fast-photosynthesizing, dense forest on loam.

Due to the returning fire, the simulated area became a mosaic of stands with various times after the stand-replacing disturbance. Started on uniform bare ground, the simulations with fire establish equilibria of species composition (Fig. 5). Since fire-return intervals on loam and sand are short, the early successional species (TA on loam and JP on sand) persist as the dominant species (compare with the trajectories of species composition

without fire: Fig. 3a, d). On clay, the area is dominated by the late-successional species, BS, as the fire return interval on the wet soil is long and the early successional stages in the nutrient-poor environment are merely ephemeral.

Comparison against field observation

The simulated dynamics of LAI on loam and clay are compared with field observations made at chronosequence sites in northern Manitoba (Bond-Lamberty et al. 2002). We assume that the simulation on loam represents “dry” stands and clay for “wet” stands of the field study. On both dry (loam) and wet (clay) soil types, ED1.0 reproduces general forest growth patterns after stand-replacing disturbance and equilibrium LAI of mature stands, with some discrepancies (Fig. 6). In both dry and wet stands, the predicted LAI of mature forests is excellent reproductions of the oldest chronosequence values at age 131. In wet stands, the field study indicates that understorey species such as shrubs, herbs, and mosses constitute a large fraction of LAI in early successional stages, and the total ecosystem LAI around three establishes very quickly after the disturbance due to the rapid growth of understorey species. Since these understorey species are not represented in this study, the LAI trajectory for wet stand underestimates the rate of initial LAI increase.

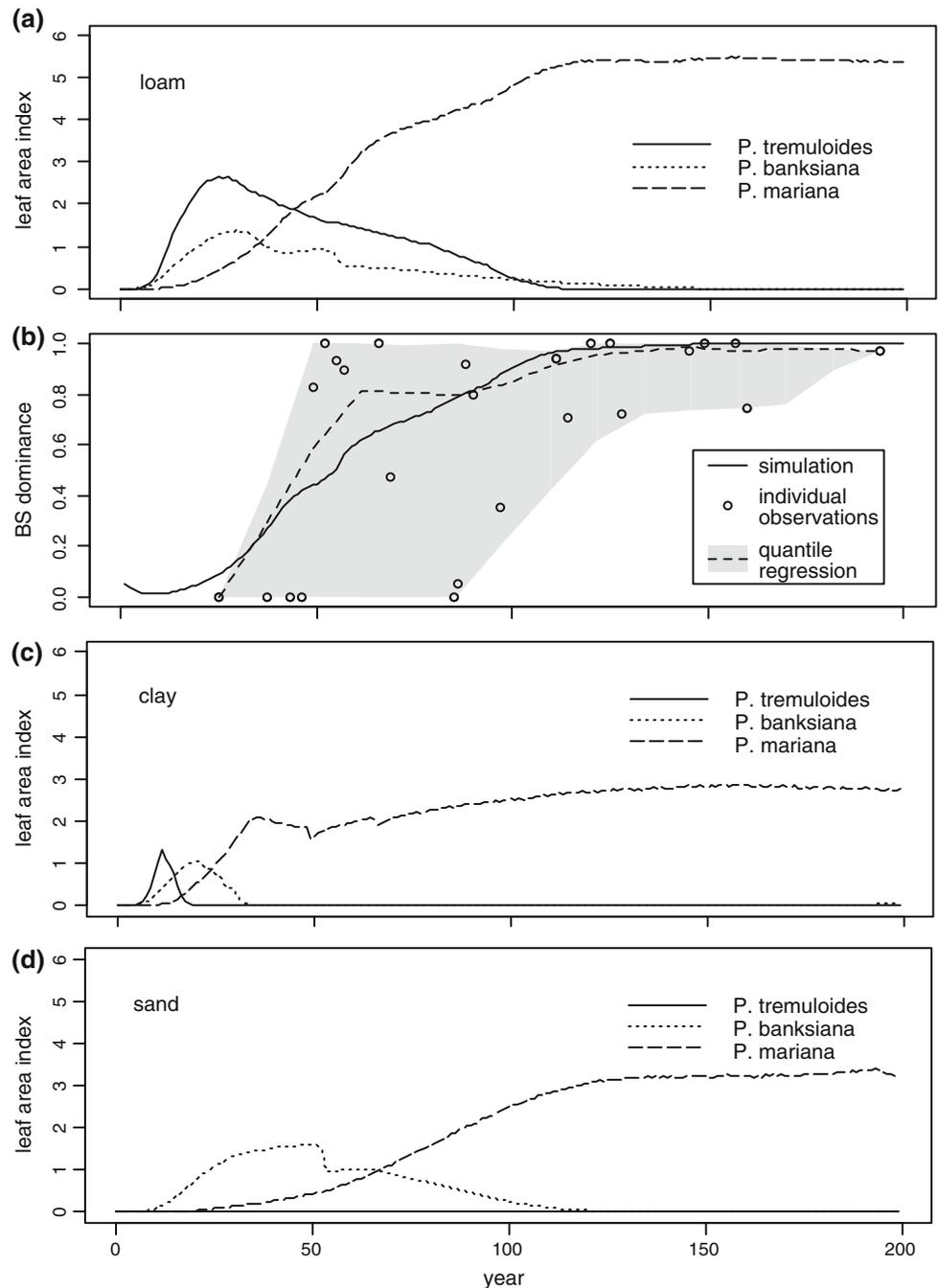
Climate change experiments

Predicted atmospheric conditions for the end of the 21st century given by GFDL R30 are used to force experimental simulations. To single out effects of changes in temperature and CO₂ concentration, we alter temperature and CO₂ concentrations separately, in addition to the simultaneous change (Fig. 7). The effect of temperature rise on forest growth is negative to both loam and clay, due to increase in aridity and autotrophic respiration. CO₂ fertilization effect is prominent on loam, but negligible on clay. Overall, the atmospheric changes have a positive effect on tree growth on loam, but not on clay.

Effects of CO₂ enrichment

To assess the effect of CO₂ enrichment to enhance vegetation growth, we make a set of experimental simulations by manipulating CO₂ concentrations, while keeping temperature and precipitation constant to 2005 values (Fig. 8). On nutrient-rich loam, the increase in atmospheric CO₂ concentration causes a significant enhancement on vegetation growth, especially for TA, a resource-demanding species (Fig. 8a, c). However, on nutrient-poor clay, the effect of CO₂ concentration change is negligible (Fig. 8b, d). Overall, these experimental simulations show that CO₂ fertilization is highly dependent on species and soil nutrient status.

Fig. 3 Simulated dynamics of leaf area index (LAI) of trembling aspen (*P. tremuloides*), jack pine (*P. banksiana*), and black spruce (*P. mariana*), in 200 years after stand-replacing disturbance, with gap dynamics. **a** Succession on loam, **c** clay, and **d** sand. July LAI of each year is plotted to represent the growing season leaf areas. **b** Dominance of the late-successional species, black spruce: comparison between simulation on loam and observation. In addition to individual observations (*open dots*), piecewise quantile regression lines are added; the *dotted line* represents 50-percentile regression, and the *shaded area* is bounded by 10-percentile (*lower bound*) and 90-percentile (*upper bound*) regression lines



Regional simulations

In addition, regional simulation of forest dynamics under both current and future climatic conditions are compared (Fig. 9). Where clay, accompanied with low soil N, is the primary soil texture (Fig. 9b), growth enhancement due to the changes in temperature, precipitation, and CO₂ concentration is negligible if not slightly negative (see Supplementary Figure 1a, b for animated transient dynamics and Supplementary Figure 2 for the shift in species composition due to the atmospheric change).

Discussion

The three boreal forest species, TA, JP, and BS show distinctive patterns of competition and succession on three soil types—loam, clay, and sand. The variation in forest dynamics in heterogeneous environment are essentially driven by physiological responses of forest species to resources such as sunlight, water, and mineralized nitrogen. ED1.0 successfully simulates a wide range of successional variations based on ecophysiology and environmental constraints.

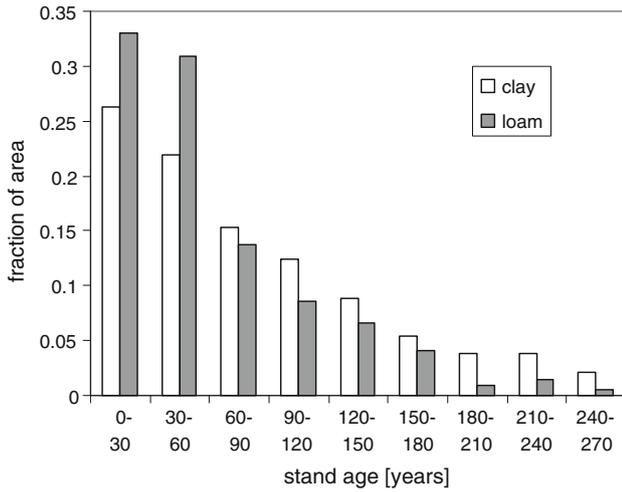


Fig. 4 Distribution of stand ages on two drainage classes (clay and loam), arisen from the simulated stand-replacing fire

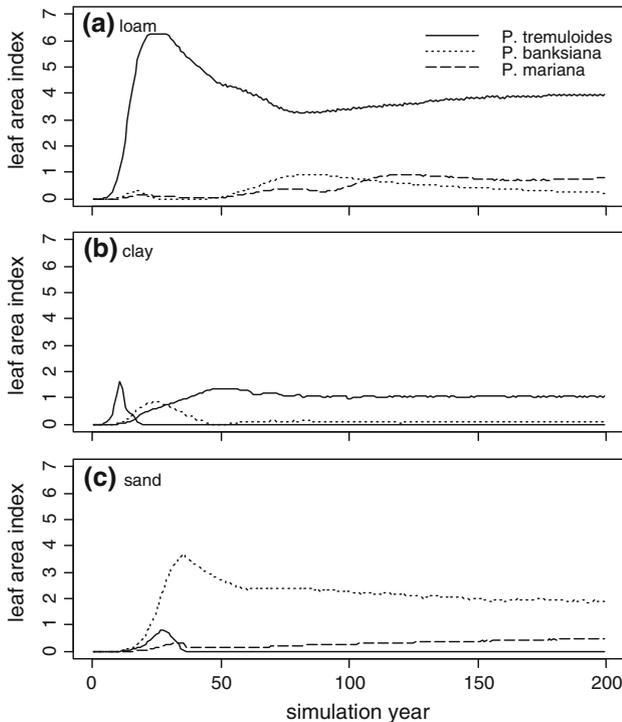


Fig. 5 Trajectories of leaf area index during spin-up and evolution of equilibrium distributions of three species: trembling aspen (*P. tremuloides*), jack pine (*P. banksiana*), and black spruce (*P. mariana*). Due to the variation in fire-return interval, three different soil types, **a** loam, **b** clay, and **c** sand, have different stand age distributions, and the resultant species composition. On loam and sand, in equilibria, the fractions of area covered by early successional species are large, compared to the old-growth dominated stands on clay

On nutrient-rich loam, the effect of CO₂ fertilization is significant in this study. However, the magnitude of fertilization is greatly reduced from Albani et al. (2006) in which CO₂ fertilization due to the increase from the pre-industrial ca. 280 ppm to the current ca. 370 ppm

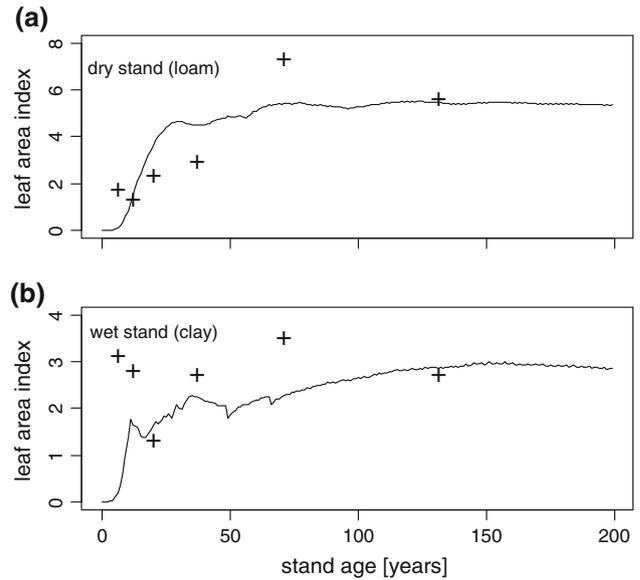


Fig. 6 Comparison of simulated (*lines*) and observed (+: Bond-Lamberty et al. 2002) leaf area index (*LAI*) through time. **a** Simulated LAI on loam is compared with observation at dry stand. **b** Simulated LAI on clay is compared with observation at wet stand

caused a 42% difference in CO₂ uptake by the forests in eastern United States. Although both the current study and Albani et al. (2006) are based on ED1.0, the consideration of nutrient limitation in this study largely reduces CO₂ fertilization effect when (1) the dominant species is slowly growing conifers and (2) the available soil nitrogen is severely limited. For example, the nutrient-poor clay prohibits growth enhancement under the future climatic conditions (Fig. 7). This reduction in growth enhancement due to soil nutrient limitation is also observed in field experimental studies (Oren et al. 2001).

Effects of CO₂ fertilization are dynamically changing through time after the disturbance. The initial effect of CO₂ fertilization on early successional species is strong; the maximum TA LAI on loam increases from 2.8 to 5.4 when CO₂ concentration is high (Fig. 8). However, as soil-mineralized nitrogen becomes incorporated into living biomass and organic matter, the growth rate of late-successional species is gradually controlled by nutrient availability, instead of CO₂ concentration, even on nutrient-rich loam.

The growth enhancement by 2100 atmospheric forcings shown in the regional simulations is mainly from CO₂ fertilization. On both loam and clay, the simulations with 2100 temperature and 2005 CO₂ concentration reveal that the effect of temperature rise is in fact negative (Fig. 7), except for a transient (years 50–80) growth enhancement on loam. The possible mechanisms of growth decline under warmer conditions include evapotranspirational losses of soil moisture and depletion of soil mineralized nitrogen due to the fast metabolism (Way and Sage 2008). These patterns can be elucidated by further analyses in soil moisture and nitrogen dynamics.

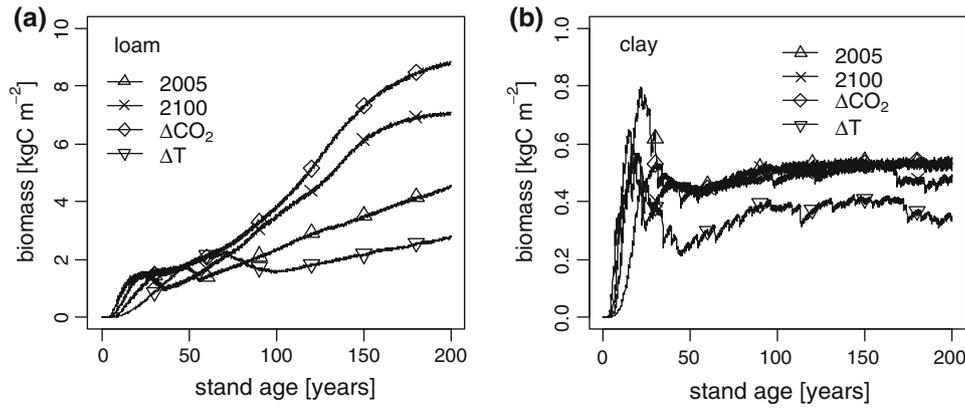
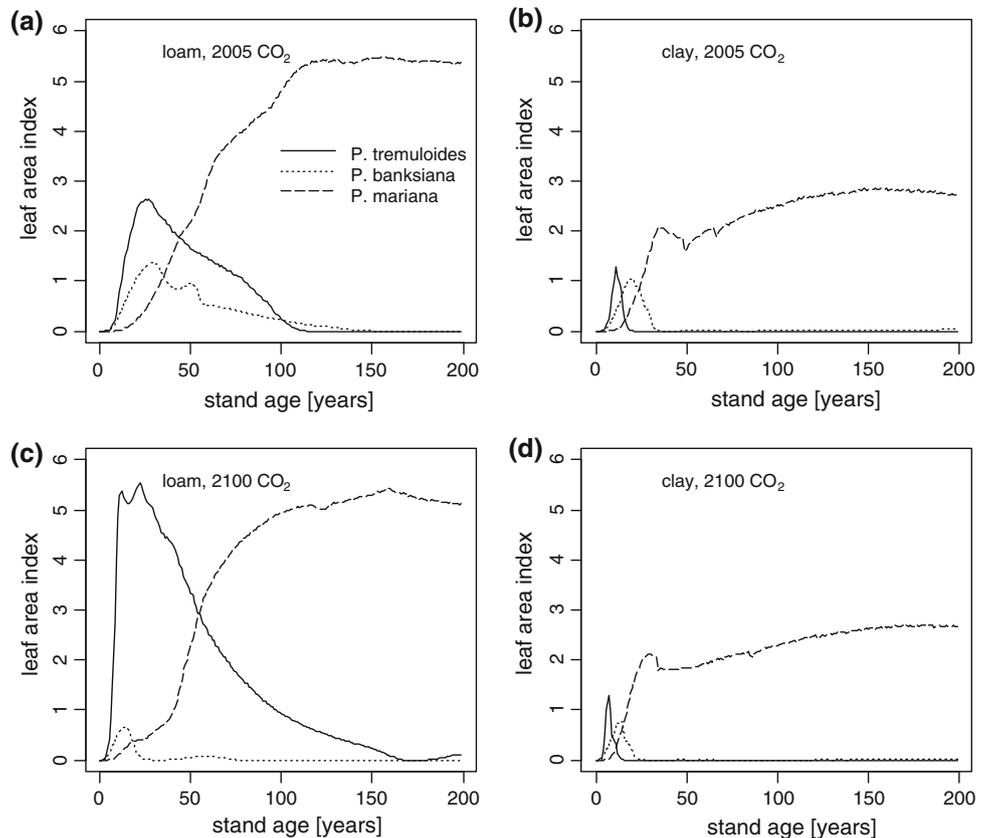


Fig. 7 Effects of atmospheric changes on forest biomass. **a** Loam and **b** clay. 2005 Denotes simulations forced by 2005 climate and atmospheric CO₂ concentration. 2100 denotes simulations forced by 2100 climate and atmospheric CO₂ concentration. ΔCO₂

denotes simulations forced by 2100 CO₂ concentration while temperature and precipitation are kept at 2005 levels. ΔT denotes simulations forced by 2100 temperature while CO₂ concentration and precipitation are kept at 2005 levels

Fig. 8 Effects of CO₂ fertilization on two soil types, for trembling aspen (*P. tremuloides*), jack pine (*P. banksiana*), and black spruce (*P. mariana*). **a** On loam with 2005 CO₂ concentration. **b** On clay with 2005 CO₂ concentration. **c** On loam with 2100 CO₂ concentration. **d** On clay with 2005 CO₂ concentration. Monthly temperature and precipitation of 2005 are used in all simulations



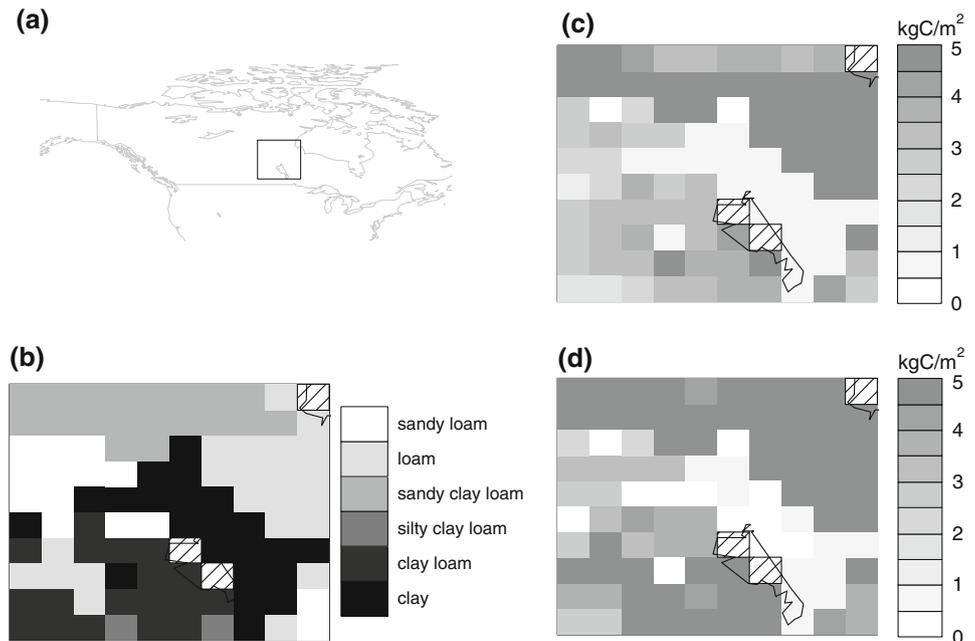
Although ED1.0 reproduces the reasonable LAI of mature stands, it does not show the transient overshoot in LAI at the time of maturation observed in the field (Fig. 6). The overshoot and minor decline in forest productivity are noticed in classic ecological studies (e.g., Kira and Shidei 1967; Odum 1969), and this trend has been thought to be caused by the gradual change in relative magnitudes of gross photosynthetic production and respirational costs such as maintenance of woody tissue. In future studies, adjustments in carbon and

nitrogen allocation in the model (Litton et al. 2007), in addition to changes in mortality according to tree ages, can reproduce the overshoot and the time lag to achieve the equilibrium.

Ecosystem demography model version 1.0 can potentially be applied to other boreal regions because the model explicitly represents basic ecological processes in boreal forests such as fire and succession pathways along resource gradients. For example, ED1.0 can easily be parameterized to simulate forest

Fig. 9 Regional simulations of changes in total above-ground biomass after 200 years.

a Location of the extent of simulation (50–60°N and 94–104°W; 1° resolution). **b** Map of soil texture in the region. Simulations with meteorological inputs (monthly temperature, precipitation, and CO₂ concentration) of **c** 2005 and **d** 2100. All simulations were started from bare ground and allowed to establish dynamic equilibria under the given meteorological conditions, with fire disturbance. *Hatched* cell are mainly covered by open water



dynamics in Eastern Siberia, one of the largest forested areas of the world. To do this, species-specific parameters of larch [*Larix gmelinii* (Rupr.) Rupr. and *L. cajanderi* Mayr.], the dominant species of the area, should be obtained from field-based studies (e.g., Usoltsev 2002), and model performance can be tested against pre-existing field observation and/or remote sensing studies (e.g., Suzuki et al. 2007). Future application of ED1.0 in pan-Arctic boreal regions will help estimate impacts of global environmental change onto boreal ecosystem function such as carbon storage/release dynamics.

Conclusion

The real boreal forest dynamics is largely affected by environmental variations, and this simulation study integrates that effect in a mechanistic way. As a result, the transient dynamics and equilibrium forest structure emerged from the model are largely consistent with the wide variety of field observations. Changes in climate and CO₂ concentrations are exerting strong effects on plant physiology and the resultant forest dynamics. The magnitude of CO₂ fertilization is dependent on soil fertility, and temperature rise can decrease plant carbon balances. These responses are highly variable depending on environment, and large-scale models should explicitly treat the heterogeneity.

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References

- Albani M, Medvigy D, Hurtt GC, Moorcroft PR (2006) The contributions of land-use change, CO₂ fertilization, and climate variability to the Eastern US carbon sink. *Glob Change Biol* 12:2370–2390
- Apps MJ, Halliwell D (1999) BOREAS TE-13 biometry reports. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA. <http://www.daac.ornl.gov>
- Bond-Lamberty B, Wang C, Gower ST (2002) Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Can J For Res* 32:1441–1450
- Brubaker LB (1975) Postglacial forest patterns associated with till and outwash in north-central upper Michigan. *Quat Res* 5:499–527
- Chipman SJ, Johnson EA (2002) Understory vascular plant species diversity in the mixedwood boreal forest of western Canada. *Ecol Appl* 12:588–601
- Clapp RB, Hornberger GM (1978) Empirical equations for some soil hydraulic-properties. *Water Resour Res* 14:601–604
- Curtis PS, Wang XZ (1998) A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113:299–313
- Delworth TL, Stouffer RJ, Dixon KW, Spelman MJ, Knutson TR, Broccoli AJ, Kushner PJ, Wetherald RT (2002) Review of simulations of climate variability and change with the GFDL R30 coupled climate model. *Clim Dyn* 19:555–574
- Dingman SL (2002) Physical hydrology, 2nd edn. Prentice-Hall, Upper Saddle River, NJ, p 600
- Farquhar GD, Sharkey TD (1982) Stomatal conductance and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 33:317–345

- Global Soil Data Task (2000) Global soil data products CD-ROM (IGBP-DIS). International Geosphere-Biosphere Programme—data and information services. ORNL Distributed Active Archive Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA. <http://www.daac.ornl.gov/>
- Greene DF, Johnson EA (1999) Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. *Can J For Res* 29:462–473
- Holland MM, Bitz CM (2003) Polar amplification of climate change in coupled models. *Clim Dyn* 21:221–232
- Host GE, Pregitzer KS (1992) Geomorphic influences on ground-flora and overstory composition in upland forests of north-western lower Michigan. *Can J For Res* 22:1547–1555
- IPCC (2001) Climate change 2001: the scientific basis. http://www.grida.no/climate/ipcc_tar/
- Ise T, Moorcroft PR (2006) The global-scale temperature and moisture dependencies of soil organic carbon decomposition: an analysis using a mechanistic decomposition model. *Biogeochemistry* 80:217–231
- Johnson EA, Miyaniishi K, Weir JMH (1995) Old-growth, disturbance, and ecosystem management. *Can J Bot* 73:918–926
- Kira T, Shidei T (1967) Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. *Jpn J Ecol* 117:70–81
- Larsen CPS (1997) Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *J Biogeogr* 24:663–673
- Le Goff H, Sirois L (2004) Black spruce and jack pine dynamics simulated under varying fire cycles in the northern boreal forest of Quebec. *Canada Can J For Res* 34:2399–2409
- Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Glob Change Biol* 13:2089–2109
- Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin FS (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431:440–443
- Mann DH, Fastie CL, Rowland EL, Bigelow NH (1995) Spruce succession, disturbance, and geomorphology on the Tanana River floodplain, Alaska. *Ecoscience* 2:184–199
- McLeod AR, Long SP (1999) Free-air carbon dioxide enrichment (FACE) in global change research: a review. *Adv Ecol Res* 28:1–56
- Moorcroft PR, Hurtt GC, Pacala SW (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecol Monogr* 71:557–585
- New M, Hulme M, Jones PD (2000) Global 30-year mean monthly climatology, 1961–1990 data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA. <http://www.daac.ornl.gov>
- Odum EP (1969) Strategy of ecosystem development. *Science* 164:262–270
- Oren R, Ellsworth DS, Johnsen KH, Phillips N, Ewers BE, Maier C, Schafer KVR, McCarthy H, Hendrey G, McNulty SG, Katul GG (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* 411:469–472
- Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol Monogr* 66:1–43
- Pennanen J, Greene DF, Fortin MJ, Messier C (2004) Spatially explicit simulation of long-term boreal forest landscape dynamics: incorporating quantitative stand attributes. *Ecol Model* 180:195–209
- Randerson JT, Liu H, Flanner MG, Chambers SD, Jin Y, Hess PG, Pfister G, Mack MC, Treseder KK, Welp LR, Chapin FS, Harden JW, Goulden ML, Lyons E, Neff JC, Schuur EAG, Zender CS (2006) The impact of boreal forest fire on climate warming. *Science* 314:1130–1132
- Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Bushena C (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct Ecol* 12:327–338
- Rich PM, Fournier R (1999) BOREAS TE-23 map plot data. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA. <http://www.daac.ornl.gov>
- Sato H, Itoh A, Kohyama T (2007) SEIB-DGVM: a new dynamic global vegetation model using a spatially explicit individual-based approach. *Ecol Model* 200:279–307
- Sellers P, Hall F, Margolis H, Kelly B, Baldocchi D, Denhartog G, Cihlar J, Ryan MG, Goodison B, Crill P, Ranson KJ, Lettenmaier D, Wickland DE (1995) The boreal ecosystem-atmosphere study (BOREAS)—an overview and early results from the 1994 field year. *Bull Am Meteorol Soc* 76:1549–1577
- Serreze MC, Walsh JE, Chapin FS, Osterkamp T, Dyurgerov M, Romanovsky V, Oechel WC, Morison J, Zhang T, Barry RG (2000) Observational evidence of recent change in the northern high-latitude environment. *Clim Change* 46:159–207
- Shiklomanov IA, Krestovsky OI (1988) The influence of forests and forest reclamation practice on streamflow and water balance. In: Reynolds ERC, Thompson FB (eds) *Forests, climate, and hydrology: regional impacts*. United Nations University Press, Tokyo, p 227
- Smith WB, Brand GJ (1983) Allometric biomass equations for 98 species of herbs, shrubs, and small trees. Research Note NC-299. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN, USA
- Soja AJ, Tchepakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Varfenova EI, Chapin FS, Stackhouse PW (2007) Climate-induced boreal forest change: predictions versus current observations. *Glob Planet Change* 56:274–296
- Suzuki R, Masuda K, Dye DG (2007) Interannual covariability between actual evapotranspiration and PAL and GIMMS NDVIs of northern Asia. *Remote Sens Environ* 106:387–398
- Thonicke K, Venevsky S, Sitch S, Cramer W (2001) The role of fire disturbance for global vegetation dynamics: coupling fire into a dynamic global vegetation model. *Glob Ecol Biogeogr* 10:661–677
- Thornthwaite CW, Mather JR (1957) The water balance. *Publ Clim* 8:1–104
- Turner MG, Tinker DB, Romme WH, Kashian DM, Litton CM (2004) Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7:751–775
- Usoltsev VA (2002) Forest biomass of Northern Eurasia: Mensuration standards and geography. Scientific Issue (in Russian), Ural Branch. Russ. Acad. Sci., Yekaterinburg, Russia
- Veldhuis H (2000) BOREAS TE-20 NSA soil lab data. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA. <http://www.daac.ornl.gov>
- Way DA, Sage RF (2008) Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.]. *Glob Change Biol* 14:624–636
- Whittaker RH, Niering WA (1975) Vegetation of Santa Catalina Mountains, Arizona. 5. Biomass, production, and diversity along elevation gradient. *Ecology* 56:771–790
- Wolf A, Callaghan TV, Larson K (2008) Future changes in vegetation and ecosystem function of the Barents Region. *Clim Change* 87:51–73

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