JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 111, G02014, doi:10.1029/2005JG000123, 2006

Simulation of boreal black spruce chronosequences: Comparison to field measurements and model evaluation

Ben Bond-Lamberty,[1] Stith T. Gower,[1] Michael L. Goulden,[2] and Andrew McMillan[2]

Received 3 November 2005; revised 28 February 2006; accepted 8 March 2006; published 8 June 2006.

[1] This study used the Biome Biogeochemical Cycles (Biome-BGC) process model to simulate boreal forest dynamics, compared the results with a variety of measured carbon content and flux data from two boreal chronosequences in northern Manitoba, Canada, and examined how model output was affected by water and nitrogen limitations on simulated plant production and decomposition. Vascular and nonvascular plant growth were modeled over 151 years in well-drained and poorly drained forests, using as many site-specific model parameters as possible. Measured data included (1) leaf area and carbon content from site-specific allometry data, (2) aboveground and belowground net primary production from allometry and root cores, and (3) flux data, including biometry-based net ecosystem production and tower-based net ecosystem exchange. The simulation used three vegetation types or functional groups (evergreen needleaf trees, deciduous broadleaf trees, and bryophytes). Model output matched some of the observed data well, with net primary production, biomass, and net ecosystem production (NEP) values usually (50–80% of data) within the errors of observed values. Leaf area was generally underpredicted. In the simulation, nitrogen limitation increased with stand age, while soil anoxia limited vascular plant growth in the poorly drained simulation. NEP was most sensitive to climate variability in the poorly drained stands. Simulation results are discussed with respect to conceptual issues in, and parameterization of, the Biome-BGC model.

Citation: Bond-Lamberty, B., S. T. Gower, M. L. Goulden, and A. McMillan (2006), Simulation of boreal black spruce chronosequences: Comparison to field measurements and model evaluation, *J. Geophys. Res.*, *111*, G02014, doi:10.1029/2005JG000123.

1. Introduction

[2] The large area, high soil carbon content, and projected warming of the circumpolar boreal forest emphasize the importance of studying boreal carbon and nitrogen cycles [*Apps et al.*, 1993; *Schulze et al.*, 1999; *Gower et al.*, 2001; *Schimel et al.*, 2001]. Elucidating the links between fire, soil drainage and temperature, and carbon and nutrient cycling will require a range of scientific techniques, including biometry-based inventories, CO_2 flux measurements using both chamber and eddy covariance methods, and computer modeling [*Stocks et al.*, 1996; *Running et al.*, 1999; *Wan et al.*, 2001; *Wirth et al.*, 2002].

[3] The chronosequence approach, a space-for-time substitution, is useful for studying changes in ecosystem structure and function during succession [*Powers and Van Cleve*, 1991], but controlling site-to-site variability, and ensuring that such variability is not mistakenly identified as temporal change, can be difficult. Computer modeling complements field data by identifying key parameters that strongly influence ecosystem structure and function, and testing processes under changing environmental conditions; field measurements can identify weaknesses in the model. Researchers need to quantify a model's performance at a local scale, and over the entire life of a forest stand, before expanding the spatial area under consideration [*Amthor et al.*, 2001; *Luckai and Larocque*, 2002].

[4] The goal of this study was to compare simulated forest dynamics to field measurements from well-drained and poorly drained boreal chronosequences in Manitoba, Canada. These chronosequences encompass the mean fire return interval for the region, have been extensively studied, and are representative of a larger group of stands samples throughout central Manitoba [*Bond-Lamberty et al.*, 2004]. The goals of this study were to (1) simulate both vascular and nonvascular plant growth and forest succession in well-drained and poorly drained boreal stands, using the process model Biome-BGC, and compare model output to a variety of field data; and (2) examine how model output was affected by water and nitrogen limitations on simulated plant production and decomposition. Simulation results are discussed with respect to conceptual issues in, and parameterization of, the model.

2. Methods

2.1. Site Descriptions

[5] The study was conducted in a black spruce (*Picea mariana* (Mill.) BSP)-dominated wildfire chronosequence

[1]Department of Forest Ecology and Management, University of Wisconsin, Madison, Wisconsin, USA.
[2]Earth System Science and Ecology and Evolutionary Biology, University of California, Irvine, Irvine, California, USA.

0148-0227/06/2005JG000123$09.00

west of Thompson, Manitoba, Canada, near the BOREAS Northern Study Area (55°53′N, 98°20′W). The chronosequence consisted of seven different-aged forests, all of which originated from stand-killing wildfire; the oldest stand in the chronosequence (151 years) is the BOREAS NSA tower site [*Sellers et al.*, 1997]. Poorly drained and well-drained stands were located in each different-aged forest. The stands have been extensively studied and differed in their species mix and leaf area [*Bond-Lamberty et al.*, 2002b], canopy transpiration [*Ewers et al.*, 2005], carbon [*Wang et al.*, 2003; *Manies et al.*, 2005] and nitrogen [*Bond-Lamberty et al.*, 2006] distribution, and net primary and ecosystem production [*Gower et al.*, 1997; *Goulden et al.*, 1998; *Litvak et al.*, 2003; *Bond-Lamberty et al.*, 2004].

[6] The stands were dominated by three tree species: trembling aspen (*Populus tremuloides* Michx) and jack pine (*Pinus banksiana* Lamb.) in the younger well-drained stands, and black spruce, the climax vegetation type, in the older stands. In the well-drained stands, the black spruce canopy closure, at 50–60 years, is associated with drastic thinning of the understory and growth of thick feather mosses (usually *Ptilium*, *Pleurozium* or *Hylocomium* spp.); in the poorly drained stands, the canopy remains open, with black spruce, Labrador tea (*Ledium groenlandicum* Oeder), and *Sphagnum* spp. dominating production; jack pine can be found on well-drained hummocks. This succession pattern is typical of much of the western North American boreal forest [*Viereck*, 1983].

[7] Study sites were carefully selected to minimize differences in soil type. Moderately drained montmorillonite clays classified as Gray Luvisols (Boralfs) dominated the uplands; the poorly drained stands' soils were Terric Fibrisols and Terric Humisols (Terric Cryofibrists and Terric Cryosaprists), associated with Luvic Gleysols (Aqualfs), Terric Fibric Organic Cryosols, and Terric Humic Organic Cryosols (Terric Fibristels and Terric Sapristels). Discontinuous permafrost occurred at 75–100 cm.

2.2. Model Description

[8] Biome-BGC is a process-based ecophysiological model that uses daily meteorological data, ecophysiological parameters, and general stand soil information to simulate energy, carbon (C), water, and nitrogen (N) cycling [*Running and Hunt*, 1993; *White et al.*, 2000]. Leaf area index controls canopy radiation absorption; a Farquhar model simulates photosynthesis, with CO_2 and water vapor diffusivity that are functions of vapor pressure deficit, temperature, and water limitations [*Running and Coughlan*, 1988]. Ecophysiological parameters define vegetation types, descriptions based on leaf habit, photosynthesis pathway, plant type, etc., that are intended to be broadly significant. The version of Biome-BGC used here was based on the 4.1.2 version but extensively modified. These changes allowed Biome-BGC to simulate multiple vegetation types concurrently, allowing for succession as well as understory/overstory dynamics [*Bond-Lamberty et al.*, 2005], more accurately track boreal soil temperatures, and account for the deleterious effects of poor soil drainage on soil decomposition and vascular plant growth, while simulating nonvascular (bryophyte) plant growth (B. Bond-Lamberty et al., Improved simulation of poorly drained forests using Biome-BGC, submitted to *Tree Physiology.*, 2006) (hereinafter referred to as Bond-Lamberty et al., submitted manuscript, 2006).

[9] Water and nitrogen (N) strongly control plant growth both in the boreal forest and most ecophysiological models [*Hobbie et al.*, 2002; *Liu et al.*, 2005]. In the version of Biome-BGC used here, soil water inflow is a function of daily precipitation and a parameter that determines how much additional water will arrive via lateral inflow for every unit of precipitation [cf. *Zhang et al.*, 2002]. Water leaves the soil pool via surface and groundwater outflow, transpiration, and evaporation from the soil surface (B. Bond-Lamberty, submitted manuscript, 2006). No vertical soil processes or differentiation is recognized. Nitrogen enters the system via deposition or fixation, both fixed-rate processes that occur irrespective of plant activity or meteorological conditions. It is lost via fire (a fixed-rate process), leaching (a function of water outflow), and denitrification: On each day, a fixed proportion of excess mineral N (not required for plant growth or microbial growth) is lost. Autotrophic production is constrained via both available soil N (as compared to plant N requirement for growth) and leaf N (which scales down the maximum Rubisco carboxylation capacity). N mineralization is constrained by soil temperature and water content. Other inner processes and logic of Biome-BGC have been discussed in detail previously [*Running and Coughlan*, 1988; *Running and Gower*, 1991; *Kimball et al.*, 1997; *Bond-Lamberty et al.*, 2005] and are not discussed here.

2.3. Assessing Error and Simulated-Observed Agreement

[10] The ensembling method of *Thornton et al.* [2002] was used to quantify and remove the effects of interannual climate variability in all simulations. This factors out the relative timing of disturbance (here wildfire, just before the beginning of the simulation) vis-à-vis climate variation by taking the mean of an ensemble of simulations, with each commencing at a different year in the meteorological data file. The effect of climate variability on any output variable was computed as the coefficient of variability, equal to the standard deviation divided by the mean (N = 20). Percentages given in the results refer to this term (labeled CV_{MET} below). Simulated and observed results were compared by (1) computing the percentage of points for which the simulated interannual error, computed as described above, fell within measured plot-to-plot (spatial) error, and (2) examining linear regressions between simulated and observed data. Regression performance was assessed using adjusted R^2, residual distribution, and by testing for zero intercept and 1:1 slope lines.

2.4. Model Data Sources: Site, Soil, and Meteorological Parameters

[11] Site-specific parameters (Table 1) follow values of Bond-Lamberty et al. (submitted manuscript, 2006), which were based on work by *Amthor et al.* [2001] and *Kimball et al.* [1997]. A time series of atmospheric carbon dioxide (CO_2) [*Etheridge et al.*, 1998] from 1851 to 2001 was used instead of a fixed value. Nitrogen deposition was scaled by Biome-BGC using the variable atmospheric CO_2 values; its beginning and end values in Table 1 are not site-specific, but are typical of low- to medium-deposition values in the

Table 1. Site Parameters Used for Chronosequence Simulations[a]

Parameter	Value	Reference
Meteorological Data		
Mean annual air temperature, °C	−3.7 ± 1.0	
Mean January air temperature, °C	−23.5 ± 3.8	
Mean July air temperature, °C	15.6 ± 1.3	
Mean annual precipitation, mm	487.6 ± 52.7	
Mean annual rainfall, mm	317.8 ± 46.0	
Site and Soil		
Elevation, m	260.0	1
Albedo, %	10.0	2
Effective soil depth, m	0.5	3
Sand:silt:clay ratio, %	26:29:45	4
N deposition in 1850, kg N m^{-2} yr^{-1}	0.0002	5, 6
N deposition in 2001, kg N m^{-2} yr^{-1}	0.0004	5, 6, 7
N fixation, kg N m^{-2} yr^{-1}	0.0002	5, 8

[a]Meteorological data summarize the climate file used to drive the simulation, and are given as annual mean ±1 standard deviation (based on 20 years of daily data; see text). References are as follows: 1, *Halliwell and Apps* [1997]; 2, *Betts and Ball* [1997]; 3, *Steele et al.* [1997]; 4, *Burke et al.* [1997]; 5, *Landsberg and Gower* [1997]; 6, *Schlesinger* [1997]; 7, *Moore et al.* [2004]; 8, *DeLuca et al.* [2002].

Canadian boreal forest [*Landsberg and Gower*, 1997; *Moore et al.*, 2004], as is the N fixation value [*Landsberg and Gower*, 1997; *DeLuca et al.*, 2002].

[12] Initial site carbon and nitrogen conditions were set to mimic those of a mature boreal black spruce forest after stand-killing wildfire: generally, observed values from the youngest stand in the chronosequence. EN coarse woody debris values were set to 1.0 and 0.1 kg C m^{-2} in the well-drained and poorly drained sites, respectively [*Bond-Lamberty et al.*, 2002a]. We assumed complete volatilization of fine litter in fire [*Stocks and Kauffman*, 1997; *Wang et al.*, 2003]. For the well-drained simulation we used the same value for initial soil C (8.7 kg C m^{-2}, with the four soil pools containing 0.0, 0.2, 2.0, and 6.5 kg C m^{-2}) as reported by *Kimball et al.* [1997, 2000]; the poorly drained simulation's values were set at twice this value (17.4 kg C m^{-2} total).

[13] The primary source of meteorological forcing data was data from the NCEP/NCAR Reanalysis Project [*Kalnay et al.*, 1996; *Kistler et al.*, 2001]; data for the BOREAS NSA from 1980 to 1999 were used here. These 20 years' data were repeated to fill out the 151-year simulation performed here. Site-specific surface meteorological and radiation data collected during BOREAS, as well as micrometeorological stations in each chronosequence stand, were used to check that the NCEP/NCAR data accurately represented local conditions [*Bond-Lamberty et al.*, 2005].

2.5. Model Data Sources: Plant Ecophysiological Parameters

[14] Three vegetation types were simulated: evergreen needleleaf (abbreviated EN, primarily *P. mariana* in the chronosequence), deciduous broadleaf (DB, primarily *P. tremuloides*), and bryophytes (BRY; here we do not distinguish between upland feathermosses and lowland *Sphagnum* spp). Plant ecophysiological parameters are summarized in Table 2. We used values given by Bond-Lamberty et al. (submitted manuscript, 2006), with a few exceptions. Stomatal restriction due to flooding was set to 20–30% (cf. B. Bond-Lamberty et al., submitted manuscript, 2006). Fine root allocation for EN was set to 0.7 on the basis of site-specific production data [*Bond-Lamberty et al.*, 2004] (fine root NPP divided by leaf NPP). Bryophyte leaf turnover was computed from site-specific biomass and net primary production data [*Wang et al.*, 2003; *Bond-Lamberty et al.*, 2004]. We know of no study reporting bryophyte specific leaf area, and used a value (20 m^2 kg C^{-1}) intermediate between the EN and DB values. Bryophytes do not have true roots, but rather small rhizoids; fine root allocation was set to a very low value (0.05) to reflect this. Other bryophyte values (full turgor water content of 5.0; 50% external water; etc.) followed B. Bond-Lamberty et al. (submitted manuscript, 2006).

3. Results

[15] Simulated biomass (stem mass for trees, leaf mass for bryophytes) generally matched observed data in the well-drained stands (62% of simulated data within observed error; Figure 1a). Agreement between simulated and measured data was poorer in the poorly drained simulation (14% within observed error, Figure 1b); in particular, simulated EN biomass in the oldest stand was significantly (3.1 versus 1.4 kg C m^{-2}) higher than that observed by *Wang et al.* [2003]. Interannual meteorological variability (CV_{MET}) for biomass was 10–25% of the mean in the well-drained stands and 2–4% in the poorly drained stands; DB in the well-drained stands was the exception (CV_{MET} = 118%). Leaf area index (LAI) was underestimated by Biome-BGC for the two oldest well-drained stands (by ~25%), while the poorly drained stand data were matched more closely (data not shown). Biome-BGC simulated peak overstory LAI at ages 47 and 45 years for the well-drained and poorly drained stands, respectively. No bryophyte LAI data were available to check simulated bryophyte LAI, which climbed to ~3 in the well-drained stand and ~6 in the poorly drained stand. An overall assessment of model performance is shown in Table 3.

[16] Simulated net primary production (NPP) of trees with evergreen needleleaf foliage (EN) tracked observed data from the chronosequence over 151 years (the age of the oldest chronosequence stand; Figure 2). Simulated NPP of trees with deciduous broadleaf foliage (DB) matched field data from the very young stands, but Biome-BGC simulated the replacement of DB by EN prematurely (at ~40 years versus ~60 observed). Simulated bryophyte (BRY) NPP generally fell within observed variability of field measurements; one conspicuous exception was the 20-year-old poorly drained stand (Figure 2b), discussed further below. The CV_{MET} of annual NPP was 30–300% at the beginning of the simulation (early in succession), and 10–60% at the end. The NPP of deciduous broadleaf trees (DB) was much more sensitive to climate variability than were EN or BRY NPP in the well-drained stands (CV_{MET} = 148% versus 25% and 21%, respectively; data not shown).

[17] Biome-BGC simulated a negative (source to atmosphere) net ecosystem production (NEP) immediately after stand-killing wildfire, and a maximum sink of 74.8 and 72.1 g C m^{-2} yr^{-1} in the well-drained and poorly drained stands, respectively, followed by a long gradual decline. Simulated NEP matched observed values in 80% of the stands (Figure 3). Simulated NEP was closer to the tower values for the first half of the chronosequence, and closer to

Table 2. Simulation Ecophysiological Parameters, by Vegetation Type[a]

Parameter	EN	DB	BRY	References
Allocation and N Requirements				
Fine root:leaf C	1.6	1.5	0.05	1
Stem C:leaf C	2.3	2.0	n/a	1
Coarse root:stem C	0.3	0.4	n/a	1
Leaf C:N	59.6	19.8	40.0	2, 4, 5
Leaf litter C:N	90.0	34.6	87.0	2, 4, 5
Fine root C:N	60.0	19.8	40.0	2, 4
Live wood C:N	151.5	92.6	n/a	2, 4
Dead wood C:N	714.3	625.0	n/a	2, 4
Leaf litter labile:cellulose:lignin (%)	32:44:24	39:44:17	19:44:37	6
Canopy Parameters				
Leaf turnover (yr^{-1})	0.12	1.0	0.11	1, 2, 3
Whole plant mortality (yr^{-1})	0.01	0.01	0.01	1
SLA (projected area basis, $m^2\ kg^{-1}$ C)	8.3	38.7	20.0	7
All sided:projected leaf area	3.1	2.0	2.0	8
Max vegetation height (m)	15.8	13.2	0.1	6
Mass at maximum height (kg C m^{-2})	12.0	12.5	1.0	6
Leaf N in Rubisco (%)	6.0	14.0	6.0	9, 10
Cuticular conductance (mm s^{-1})	0.01	0.01	0.03	11, 12, 6
Boundary layer conductance (mm s^{-1})	80.0	20.0	50.0	12, 13
Ψ_L start of g_s reduction (MPa)	−0.5	−0.5	n/a	11, 12
Ψ_L complete g_s reduction (MPa)	−1.7	−2.3	n/a	11, 12
VPD start of g_s reduction (KPa)	1.0	1.0	n/a	11, 12
VPD complete g_s reduction (KPa)	4.1	4.0	n/a	11, 12
Flooded g_s reduction (%)	30	20	n/a	6
Days to reach g_s reduction (days)	5	5	n/a	6

[a]Vegetation types are deciduous broadleaf, DB, and evergreen needleleaf, EN. A blank reference means that the value given is the default value distributed with BIOME-BGC. Abbreviations used include C (carbon), N (nitrogen), SLA (specific leaf area), Ψ_L (leaf water potential), and VPD (vapor pressure deficit). References are as follows: 1, *Bond-Lamberty et al.* [2004]; 2, *Gower et al.* [1997]; 3, *Steele et al.* [1997]; 4, *Gower et al.* [2000]; 5, *Aerts et al.* [2001]; 6, B. Bond-Lamberty et al. (submitted manuscript, 2006); 7, *Bond-Lamberty et al.* [2002b]; 8, *Bond-Lamberty et al.* [2003]; 9, *Field and Mooney* [1986]; 10, *Fan et al.* [1995]; 11, *Kimball et al.* [1997]; 12, *Nobel* [1991]; 13, *Ewers et al.* [2005]; 14, *Proctor* [2000]; 15, *Williams and Flanagan* [1998].

the values determined by biometry in the oldest stands. In general, tower-based NEP was higher (more of a carbon sink) than was biometry-based NEP, but the two agreed with each other well, and simulated values fell within the computed errors of each. Only biometry measurements were performed in the poorly drained sites, and here simulated NEP matched the observed measurements well (Figure 3b), except in the 20-year-old poorly drained stand.

[18] Simulated NEP was affected more by interannual meteorological variability for the poorly drained chronosequence (mean CV_{MET} over 151 years of 74%) than for the well-drained one (32%). The degree to which NEP was affected by the climate data varied with stand age (Figure 4). In the younger stands ($<\sim$60 years) the well-drained simulation was more sensitive to climate variability; after this point, NEP of the poorly drained stands was much more strongly affected by climate. In particular, the oldest stands were quite vulnerable to changes in climate, particularly rainfall (CV of 81% and 116% for the well-drained and poorly drained simulations, respectively).

[19] Nitrogen limitation on plant photosynthesis increased with stand age for the well-drained and poorly drained simulations; only $\sim$60% of plant demand was satisfied in the oldest stands (Figure 5). Nitrogen pools generally tracked observed biomass data [*Bond-Lamberty et al.*, 2006], although because LAI was underestimated, simulated stand N was also low (data not shown). The simulated well-drained stand experienced frequent water constraints, with low leaf water potential triggering stomatal closure; the mean constraint was 50–60% in the oldest stands. The oldest poorly drained stands also experienced some occasional water stress (solid lines in Figure 5). Conversely, anaerobic soil conditions were never a factor in the well-drained stands, but strongly limited stomatal conductance and decomposition in the poorly drained stands. Both vascular and nonvascular plants can be negatively affected by soil flooding in this version of Biome-BGC (B. Bond-Lamberty et al., submitted manuscript, 2006), but the bryophytes never experienced reduced photosynthesis due to slow CO_2 diffusion through water (data not shown).

4. Discussion

[20] These chronosequences discussed here have been shown to be representative of a large group of regional stands [*Bond-Lamberty et al.*, 2004], but there is no guarantee that any process model, however perfectly parameterized and flawless its internal logic, could replicate each chronosequence member correctly; site selection may be incorrect, and species successional patterns tend to vary in younger stands [*Viereck*, 1983]. Thus this discussion in general does not focus on why particular stands in the chronosequence were "missed" by the model.

4.1. Model Performance Across the Chronosequence

[21] Biome-BGC's simulated NPP, biomass, and NEP were usually within the errors of observed values, within the broader range of black spruce stands examined in the region by *Bond-Lamberty et al.* [2004], and consistent with

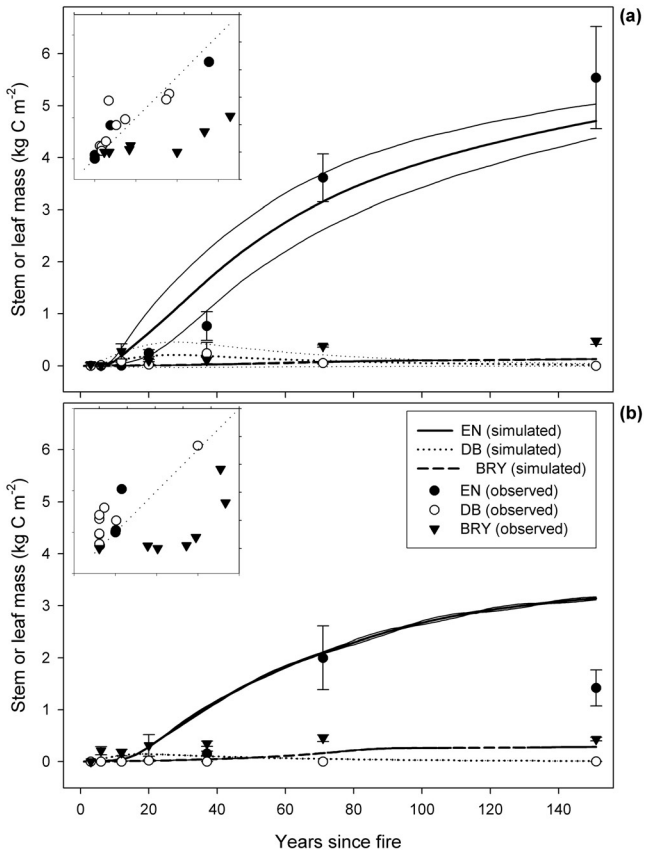

Figure 1. Chronosequence biomass, observed versus simulated, for (a) well-drained and (b) poorly drained sites, by time since fire. Three vegetation types are shown: evergreen needleleaf (EN, stem mass), deciduous broadleaf (DB, stem mass), and bryophyte (BRY, leaf mass). Thin lines bracketing main simulation lines show effect of meteorological interannual variability; error bars on observed data points represent plot-to-plot variability (N = 4 and 5 for well-drained and poorly drained stands, respectively). Inset graphs show observed (*x* axis) versus expected (*y* axis) data, with the 1:1 (dotted) line shown. For clarity, error bars are not shown in these graphs, and data series (EN, DB, BRY) may have different scales. Observed data are from *Wang et al.* [2003].

data from other studies in these stands [*Gower et al.*, 1997; *Harden et al.*, 1997; *Goulden et al.*, 1998; *Litvak et al.*, 2003] and Alaska [*O'Neill et al.*, 2003; *Zhuang et al.*, 2003]. Many commonly observed forest dynamics were seen in the simulations: net primary and ecosystem production declined after early peaks (Figures 2 and 3); bryophyte growth in the well-drained stands increased with increasing overstory leaf area; early successional deciduous trees gave way to evergreens (Figure 1). NPP and biomass were better predicted in the well-drained than in the poorly drained stands, although NEP was well predicted in both chronosequences (Table 3).

[22] In several cases, simulated and observed data diverged significantly. First, the extremely high bryophyte NPP and thus NEP of the 20-year-old poorly drained stand could not be replicated by the model (Figure 2). We argue

Table 3. Detailed Comparison Between Simulated and Observed Data, by Soil Drainage and Output Variable[a]

				H_0: $b_0 = 0$		H_0: $b_1 = 1$	
Variable	*N*	Overlap	R^2	*T*	*P*	T	*P*
Well-Drained Stands							
NPP	21	57%	0.50	0.710	0.485	−2.076	0.051
Biomass	21	62%	0.95	0.750	0.461	−3.293	0.004
LAI	14	57%	0.58	1.320	0.212	−1.972	0.070
NEP	14	85%	0.58	1.850	0.091	−6.346	<0.001
Poorly Drained Stands							
NPP	21	29%	0.00	2.760	0.012	−7.744	<0.001
Biomass	21	14%	0.73	0.100	0.918	1.806	0.086
LAI	14	36%	0.49	1.150	0.271	−0.802	0.437
NEP	7	71%	0.62	1.530	0.187	−13.993	<0.001

[a]Linear regressions (of form $y = b_0 + b_1 x$) were fit between simulated and observed data. Data reported below include number of points (*N*), percentage of points in which observed spatial error and simulated temporal errors overlap, adjusted R^2, and *T*-tests for zero intercept and 1:1 slope. Tests in which $P < 0.05$ (i.e., $b_0 \neq 0$ or $b_1 \neq 1$) are underlined for emphasis.

that this is more a failure of chronosequence site selection than of model function: bryophytes in this version of Biome-BGC are capable of up to ~500 g C m^{-2} yr^{-1} NPP (data not shown), well within the observed range, given enough water and lack of competition. However, such a stand would never develop the large tree biomass seen in the oldest poorly drained stands (Figure 1). The 20-year-old

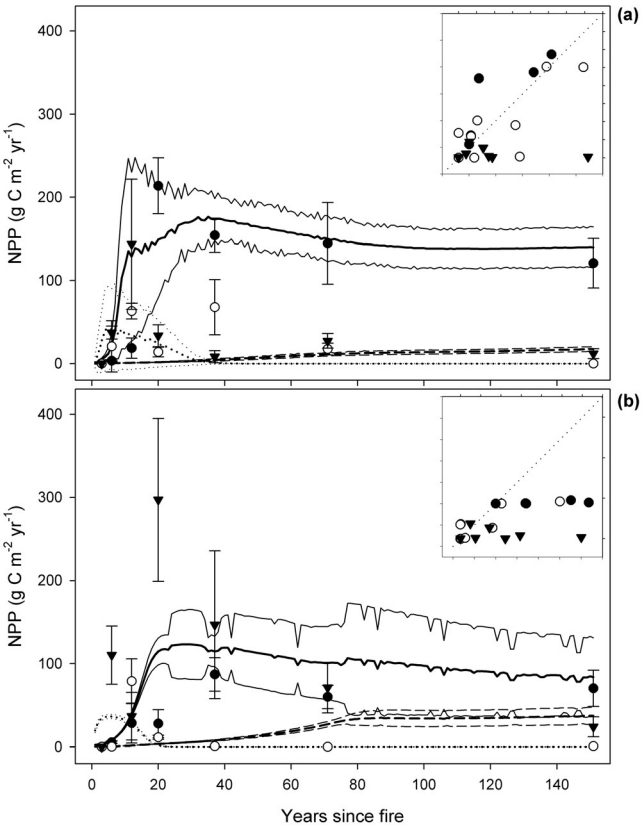

Figure 2. Net primary production (NPP), observed versus simulated, for (a) well-drained and (b) poorly drained sites, by time since fire. Symbols are as in Figure 1. Observed data are from *Bond-Lamberty et al.* [2004].

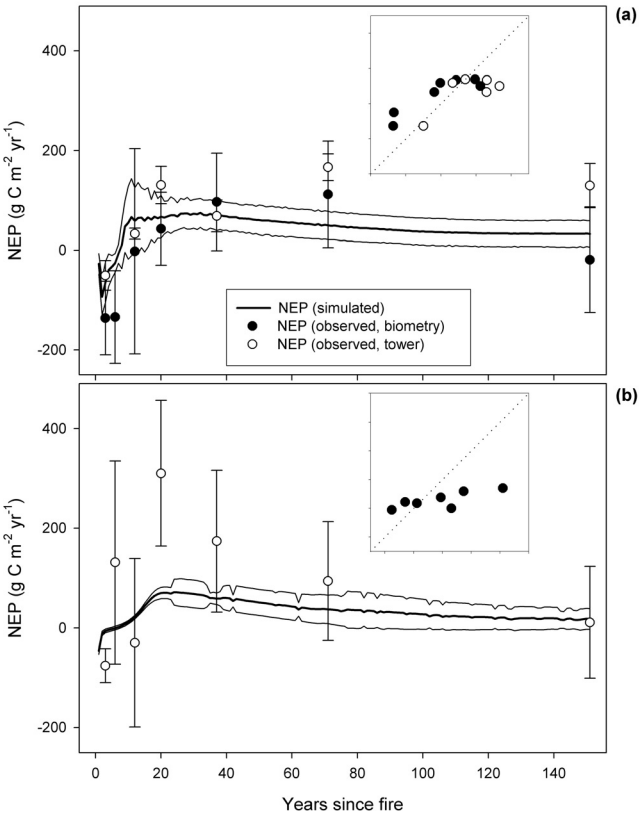

Figure 3. Net ecosystem production (NEP), observed versus simulated, for (a) well-drained and (b) poorly drained sites, by time since fire. Biometry-based NEP data are from *Bond-Lamberty et al.* [2004]; tower-based data are unpublished data (M. Goulden). Positive NEP values represent a forest carbon sink.

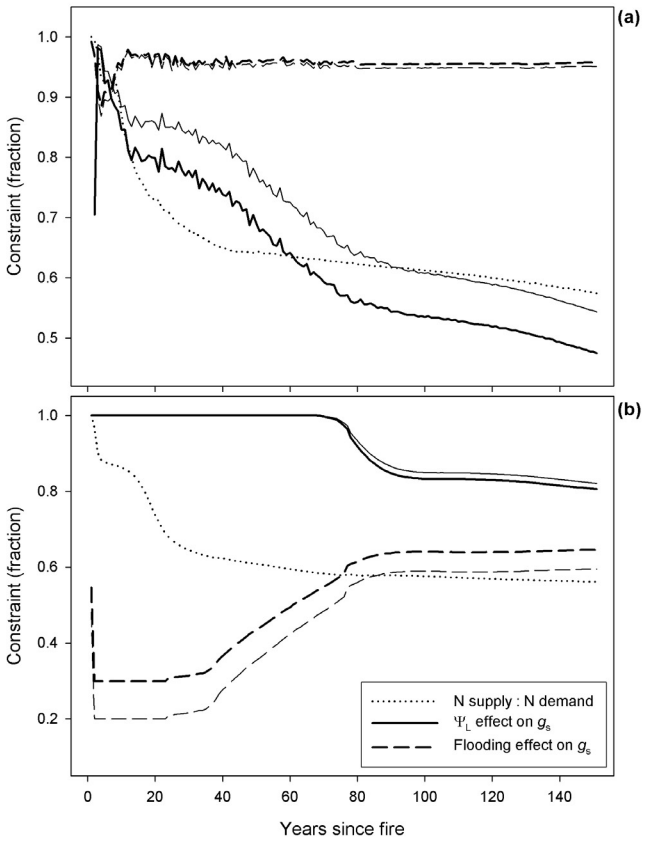

Figure 5. Degree of limitation for various factors in the (a) well-drained and (b) poorly drained chronosequences, by stand age. Factors shown include ratio of nitrogen supply to demand, leaf water potential (Ψ_L) effect on stomatal conductance (g_s), and flooding effect on g_s. In all cases, 1.0 = no limitation and 0.0 = complete limitation. Dark lines are evergreen needleleaf trees; light lines are deciduous broadleaf. Note that *y* axes have different scales.

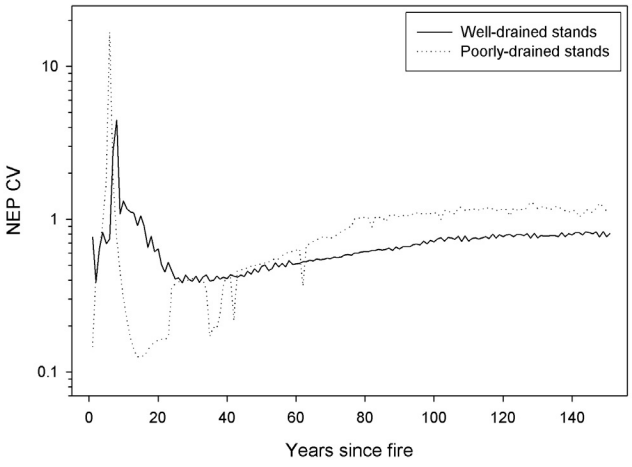

Figure 4. NEP variability (expressed as coefficient of variation or CV, equal to the standard deviation divided by the mean) for the well-drained and poorly drained chronosequences. Data were generated by repeatedly commencing simulations at each successive year in the climate file (N = 20). Note that *y* axis scale is logarithmic.

poorly drained "stand" is probably better termed a peatland, given its perennial flooded status and lack of trees [*Wang et al.*, 2003], characteristics that set it apart from the other chronosequence sites.

[23] Leaf area constituted a second problem. Biome-BGC could not replicate the EN leaf area of the oldest stands (data not shown); given how well NPP and NEP were simulated, this may suggest a problem with the internal leaf productivity and respiration parameters used in the model. In addition, we had no data on bryophyte LAI in these stands, and were unable to evaluate Biome-BGC's performance in this regard. Biomass data [*Wang et al.*, 2003] imply projected LAI values of 3–5 for the oldest chronosequence stands, if 50% of the measured biomass is leaf (at least for species such as *Pleurozium schreberi*; *Sphagnum* spp. would be almost entirely leaf) with a specific area of 20 m^2 kg^{-1} C (see Table 2). This suggests that bryophyte LAI was also underestimated by the model.

4.2. Implementation of Nitrogen Cycling in Biome-BGC

[24] The limiting role of nitrogen in the simulations (Figure 5) is consistent with its known importance in boreal

systems [*Landsberg and Gower*, 1997; *Schlesinger*, 1997; *Hobbie et al.*, 2002]. Biome-BGC uses static N fixation and deposition that belie the complexity of observed N dynamics in boreal forests [*Chapin*, 1983; *DeLuca et al.*, 2002; *Zackrisson et al.*, 2004], where the successional appearance and growth of both vascular [*Vogel and Gower*, 1998] and nonvascular [*DeLuca et al.*, 2002] species strongly affect nitrogen cycling dynamics. It is in this regard that Biome-BGC's nitrogen cycle is the least realistic, with potentially the greatest impacts on model output, as the model can be quite sensitive to these parameters [*White et al.*, 2000]. Plant growth, peat formation, and other organic matter transformations can result in significant N immobilization [*Aerts et al.*, 1999]. Biome-BGC decomposition is now retarded by excess moisture (B. Bond-Lamberty et al., submitted manuscript, 2006), but other factors important in boreal systems, for example, a seasonally changing soil active layer, are not simulated. This would have been a particular problem in the simulated poorly drained areas (see below).

4.3. Modeling Stand- and Landscape-Level Carbon Cycling of Boreal Forests

[25] The simulation data presented here suggest a number of critical areas for biogeochemical process models that are increasingly used to model landscape-level dynamics. Although evergreen needleleafs such as *Picea mariana* dominate the North American boreal forest, broadleaf deciduous trees are a significant component. In this study the interannual variability of deciduous NPP was much higher than that of evergreen or bryophyte NPP. Such interannual variability has been observed using eddy covariance flux towers [*Black et al.*, 1996; *Arain et al.*, 2002] and has implications for the realistic simulation of boreal forest dynamics, particularly under changing climate conditions and increases in boreal wildfire frequency [*Kasischke and Stocks*, 2000].

[26] In addition, interannual meteorological variability generally affected simulated NEP more strongly in the poorly drained stands than in the well-drained ones (Figure 4). The dynamics seen in this figure are the product of three effects: (1) the dominance of bryophytes in the poorly drained stands, which are vulnerable to desiccation in dry years; (2) the fragile growing conditions early in the simulation, when even small changes in meteorological conditions greatly affected the simulated tiny plants; and (3) high canopy transpiration in the older stands, which drew down soil water, thus rendering the system more vulnerable to meteorological variability. In spite of improvements (B. Bond-Lamberty et al., submitted manuscript, 2006), Biome-BGC's simple hydrology means that it remains much stronger simulating upland than lowland systems.

[27] In the context for forest carbon cycling, this implies that, over time, many simulated poorly drained areas may be highly sensitive to climate change, given their large carbon stores and delicate hydrology. Many field studies have also posited that understanding the dynamics of poorly drained systems is critical to evaluating the effects of climate change on northern ecosystems [*Van Cleve et al.*, 1986; *Freeman et al.*, 2001; *Turetsky et al.*, 2002], particularly given the large carbon storage of such systems [*Trumbore and Harden*, 1997] and their importance in global carbon cycling [*O'Neill*, 2000]. Modeling studies tend to focus on well-drained upland systems [*Kimball et al.*, 2000; *Luckai and Larocque*, 2002; *Potter*, 2004], and most process models used to simulate forest biogeochemical cycles do not deal adequately with the unique characteristics of poorly drained ecosystems [*Trettin et al.*, 2001]. All these factors argue for improved measurement and simulation of poorly drained areas.

[28] **Acknowledgments.** This research was supported by grants from the National Science Foundation (Integrated Research Challenges in Environmental Biology, DEB-0077881) and the National Aeronautics and Space Administration (NAG5-8069) to S. T. Gower. Biome-BGC version 4.1.2 was provided by the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana; NTSG assumes no responsibility for the proper use of Biome-BGC by others. The GPCP combined precipitation data were developed and computed by the NASA/Goddard Space Flight Center's Laboratory for Atmospheres as a contribution to the GEWEX Global Precipitation Climatology Project. We thank Doug Ahl for his thoughtful comments on the manuscript.

References

Aerts, R., J. T. A. Verhoeven, and D. F. Whigham (1999), Plant-mediated controls on nutrient cycling in temperate fens and bogs, *Ecology*, *80*(7), 2170–2181.

Aerts, R., B. Wallén, N. Malmer, and H. de Caluwe (2001), Nutritional constraints on *Sphagnum*-growth and potential decay in northern peatlands, *J. Ecol.*, *89*, 292–299.

Amthor, J. S., et al. (2001), Boreal forest CO_2 exchange and evapotranspiration predicted by nine ecosystem process models: Intermodal comparisons and relationships to field measurements, *J. Geophys. Res.*, *106*(D24), 33,623–33,648.

Apps, M. J., W. A. Kurz, R. J. Luxmoore, L. O. Nilsson, R. A. Sedjo, R. Schmidt, L. G. Simpson, and T. S. Vinson (1993), The changing role of circumpolar boreal forests and tundra in the global carbon cycle, *Water Air Soil Pollut.*, *70*, 39–53.

Arain, M. A., T. A. Black, A. G. Barr, P. G. Jarvis, J. M. Massheder, D. L. Verseghy, and Z. Nesic (2002), Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests, *Can. J. For. Res.*, *32*, 878–891.

Betts, A. K., and J. H. Ball (1997), Albedo over the boreal forest, *J. Geophys. Res.*, *102*(D24), 28,901–28,909.

Black, T. A., G. den Hartog, H. H. Neumann, P. D. Blanken, P. C. Yang, C. A. Russell, Z. Nesic, X. Lee, S. G. Chen, and R. M. Staebler (1996), Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest, *Global Change Biol.*, *2*, 219–229.

Bond-Lamberty, B., C. Wang, and S. T. Gower (2002a), Annual carbon flux from woody debris for a boreal black spruce fire chronosequence, *J. Geophys. Res.*, *107*, 8220, doi:10.1029/2001JD000839. [printed *108*(D3), 2003]

Bond-Lamberty, B., C. Wang, and S. T. Gower (2002b), Leaf area dynamics of a boreal black spruce fire chronosequence, *Tree Physiol.*, *22*(14), 993–1001.

Bond-Lamberty, B., C. Wang, and S. T. Gower (2003), The use of multiple measurement techniques to refine estimates of conifer needle geometry, *Can. J. For. Res.*, *33*, 101–105.

Bond-Lamberty, B., C. Wang, and S. T. Gower (2004), Net primary production and net ecosystem production of a boreal black spruce fire chronosequence, *Global Change Biol.*, *10*, 473–487.

Bond-Lamberty, B., S. T. Gower, D. E. Ahl, and P. E. Thornton (2005), Reimplementation of the BIOME-BGC model to simulate successional change, *Tree Physiol.*, *25*(4), 413–424.

Bond-Lamberty, B., C. Wang, S. T. Gower, P. Cyr, and H. Veldhuis (2006), Nitrogen dynamics of a boreal black spruce fire chronosequence, *Biogeochemistry*, in press.

Burke, R. A., R. G. Zepp, M. A. Tarr, W. L. Miller, and B. J. Stocks (1997), Effect of fire on soil-atmosphere exchange of methane and carbon dioxide in Canadian boreal sites, *J. Geophys. Res.*, *102*(D24), 29,289–29,300.

Chapin, F. S. (1983), Nitrogen and phosphorus nutrition and nutrient cycling by evergreen and deciduous understory shrubs in an Alaskan black spruce forest, *Can. J. For. Res.*, *13*, 773–781.

DeLuca, T. H., O. Zackrisson, M.-C. Nilsson, and A. Sellstedt (2002), Quantifying nitrogen-fixation in feather moss carpets of boreal forests, *Nature*, *419*, 917–920.

Etheridge, D. M., L. P. Steele, R. L. Langenfelds, R. J. Francey, J.-M. Barnola, and V. I. Morgan (1998), Historical CO_2 record from the Law

Dome DE08, DE08–2, and DSS ice cores, in Trends: A Compendium of Data on Global Change, http://cdiac.esd.ornl.gov/ftp/trends/co2/lawdome.combined.dat, Carbon Dioxide Inf. Anal. Cent. Oak Ridge, Tenn.

Ewers, B. E., S. T. Gower, B. Bond-Lamberty, and C. Wang (2005), Effects of stand age and tree species composition on transpiration and canopy conductance of boreal forest stands, *Plant Cell Environ.*, *28*, 660–678.

Fan, S.-M., M. L. Goulden, J. W. Munger, B. C. Daube, P. S. Bakwin, S. C. Wofsy, J. S. Amthor, D. R. Fitzjarrald, K. E. Moore, and T. R. Moore (1995), Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: A growing season of whole-ecosystem exchange measurements by eddy correlation, *Oecologia*, *102*, 443–452.

Field, C. B., and H. A. Mooney (1986), The photosynthesis-nitrogen relationship in wild plants, in *On the Economy of Plant Form and Function*, edited by T. J. Givnish, pp. 25–55, Cambridge Univ. Press, New York.

Freeman, C., N. Ostle, and H. Kang (2001), An enzymic "latch" on a global carbon store, *Nature*, *409*, 149.

Goulden, M. L., et al. (1998), Sensitivity of boreal forest carbon balance to soil thaw, *Science*, *279*, 214–217.

Gower, S. T., J. G. Vogel, J. M. Norman, C. J. Kucharik, S. Steele, and T. K. Stow (1997), Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada, *J. Geophys. Res.*, *102*(D24), 29,029–29,041.

Gower, S. T., A. Hunter, J. S. Campbell, J. G. Vogel, H. Veldhuis, J. W. Harden, S. E. Trumbore, J. M. Norman, and C. J. Kucharik (2000), Nutrient dynamics of the southern and northern BOREAS boreal forests, *Ecoscience*, *7*(4), 481–490.

Gower, S. T., O. N. Krankina, R. J. Olson, M. J. Apps, S. Linder, and C. Wang (2001), Net primary production and carbon allocation patterns of boreal forest ecosystems, *Ecol. Appl.*, *11*(5), 1395–1411.

Halliwell, D. H., and M. J. Apps (1997), *Boreal Ecosystem-Atmosphere Study (BOREAS) Biometry and Auxiliary Sites: Locations and Descriptions*, 120 pp., Northern For. Cent., For. Can., Edmonton, Alberta, Canada.

Harden, J. W., K. P. O'Neill, S. E. Trumbore, H. Veldhuis, and B. J. Stocks (1997), Moss and soil contributions to the annual net carbon flux of a maturing boreal forest, *J. Geophys. Res.*, *102*(D24), 28,805–28,816.

Hobbie, S. E., K. J. Nadelhoffer, and P. Högberg (2002), A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions, *Plant Soil*, *242*(1), 163–170.

Kalnay, E., et al. (1996), The NCEP/NCAR 40–year reanalysis project, *Bull. Am. Meteorol. Soc.*, *77*, 437–471.

Kasischke, E. S., and B. J. Stocks (2000), *Fire, Climate Change, and Carbon Cycling in the Boreal Forest*, 461 pp., Springer, New York.

Kimball, J. S., P. E. Thornton, M. A. White, and S. W. Running (1997), Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region, *Tree Physiol.*, *17*(8/9), 589–599.

Kimball, J. S., A. R. Keyser, S. W. Running, and S. S. Saatchi (2000), Regional assessment of boreal forest productivity using an ecological process model and remote sensing parameter maps, *Tree Physiol.*, *20*(11), 761–775.

Kistler, R., et al. (2001), The NCEP-NCAR 50–year reanalysis: Monthly means CD-ROM and documentation, *Bull. Am. Meteorol. Soc.*, *82*, 247–267.

Landsberg, J. J., and S. T. Gower (1997), *Applications of Physiological Ecology to Forest Management*, 354 pp., Elsevier, New York.

Litvak, M., S. Miller, S. C. Wofsy, and M. L. Goulden (2003), Effect of stand age on whole ecosystem CO_2 exchange in the Canadian boreal forest, *J. Geophys. Res.*, *108*(D3), 8225, doi:10.1029/2001JD000854.

Liu, J., D. T. Price, and J. M. Chen (2005), Nitrogen controls on ecosystem carbon sequestration: A model implementation and application to Saskatchewan, Canada, *Ecol. Modell.*, *186*, 178–195.

Luckai, N., and G. R. Larocque (2002), Challenges in the application of existing process-based models to predict the effect of climate change on C pools in forest ecosystems, *Clim. Change*, *55*, 39–60.

Manies, K. L., J. W. Harden, B. Bond-Lamberty, and K. P. O'Neill (2005), Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage, *Can. J. For. Res.*, *35*, 472–482.

Moore, T. R., C. Blodau, J. Turunen, N. T. Roulet, and P. J. H. Richard (2004), Patterns of nitrogen and sulfur accumulation and retention in ombotrophic bogs, eastern Canada, *Global Change Biol.*, *11*, 356–367.

Nobel, P. S. (1991), *Physiochemical and Environmental Plant Physiology*, 635 pp., Elsevier, New York.

O'Neill, K. P. (2000), Role of bryophyte-dominated ecosystems in the global carbon budget, in *Bryophyte Biology*, edited by A. J. Shaw and B. Goffinet, pp. 344–368, Cambridge Univ. Press, New York.

O'Neill, K. P., E. S. Kasischke, and D. D. Richter (2003), Seasonal and decadal patterns of soil carbon uptake and emission along an age sequence of burned black spruce stands in interior Alaska, *J. Geophys. Res.*, *108*(D1), 8155, doi:10.1029/2001JD000443.

Potter, C. S. (2004), Predicting climate change effects on vegetation, soil thermal dynamics, and carbon cycling in ecosystems of interior Alaska, *Ecol. Modell.*, *175*, 1–24.

Powers, R. F., and K. Van Cleve (1991), Long-term ecological research in temperate and boreal ecosystems, *Agron. J.*, *83*, 11–24.

Proctor, M. C. F. (2000), Physiological ecology, in *Bryophyte Biology*, edited by A. J. Shaw and B. Goffinet, pp. 225–247, Cambridge Univ. Press, New York.

Running, S. W., and J. C. Coughlan (1988), A general model of forest ecosystem processes for regional applications: I. Hydrological balance, canopy gas exchange and primary production processes, *Ecol. Modell.*, *42*, 125–154.

Running, S. W., and S. T. Gower (1991), FOREST-BGC, A general model of forest ecosystem processes for regional applications: II. Dynamic carbon allocation and nitrogen budgets, *Tree Physiol.*, *9*(1/2), 147–160.

Running, S. W., and R. E. Hunt (1993), Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models, in *Scaling Physiologic Processes: Leaf to Globe*, edited by J. R. Ehleringer and C. B. Field, pp. 141–158, Elsevier, New York.

Running, S. W., D. D. Baldocchi, D. P. Turner, S. T. Gower, P. S. Bakwin, and K. A. Hibbard (1999), A global terrestrial monitoring network, integrating tower fluxes, flask sampling, ecosystem modeling and EOS satellite data, *Remote Sens. Environ.*, *70*, 108–127.

Schimel, D. S., et al. (2001), Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems, *Nature*, *414*(6860), 169–172.

Schlesinger, W. H. (1997), *Biogeochemistry: An Analysis of Global Change*, 588 pp., Harcourt Brace, San Diego, Calif.

Schulze, E.-D., J. Lloyd, F. M. Kelliher, C. Wirth, C. Rebmann, B. Lühker, M. Mund, A. Knohl, I. M. Milyukova, and W. Schulze (1999), Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink—A synthesis, *Global Change Biol.*, *5*, 703–722.

Sellers, J., et al. (1997), BOREAS in 1997: Experiment overview, scientific results, and future directions, *J. Geophys. Res.*, *102*(D24), 28,731–28,769.

Steele, S., S. T. Gower, J. G. Vogel, and J. M. Norman (1997), Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada, *Tree Physiol.*, *17*(8/9), 577–587.

Stocks, B. J., and J. B. Kauffman (1997), Biomass consumption and behavior of wildland fires in boreal, temperate, and tropical ecosystems: Parameters necessary to interpret historic fire regimes and future fire scenarios, in *Sediment Records of Biomass Burning and Global Change*, edited by J. S. Clark et al., pp. 169–188, Springer, New York.

Stocks, B. J., B. S. Lee, and D. L. Martell (1996), Some potential carbon budget implications of fire management in the boreal forest, in *Forest Ecosystems, Forest Management and the Global Carbon Cycle*, edited by M. J. Apps, and D. T. Price, pp. 89–96, Springer, New York.

Thornton, P. E., et al. (2002), Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests, *Agric. For. Meteorol.*, *113*, 185–222.

Trettin, C. C., B. Song, M. F. Jurgenson, and C. Li (2001), Existing soil carbon models do not apply to forested wetlands, *Gen. Tech. Rep. SRS-46*, 10 pp., USDA For. Serv., Asheville, NC.

Trumbore, S. E., and J. W. Harden (1997), Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area, *J. Geophys. Res.*, *102*(D24), 28,817–28,830.

Turetsky, M. R., K. Wieder, L. A. Halsey, and D. H. Vitt (2002), Current disturbance and the diminishing peatland carbon sink, *Geophys. Res. Lett.*, *29*(11), 1526, doi:10.1029/2001GL014000.

Van Cleve, K., F. S. Chapin, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness (1986), Forest ecosystems in the Alaskan Taiga, in *Ecological Studies*, pp. 74–86, Springer, New York.

Viereck, L. A. (1983), The effects of fire in black spruce ecosystems of Alaska and northern Canada, in *The Role of Fire in Northern Circumpolar Ecosystems*, edited by R. W. Wein and D. A. MacLean, pp. 201–220, John Wiley, Hoboken, N. J.

Vogel, J. G., and S. T. Gower (1998), Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory, *Ecosystems*, *1*, 386–400.

Wan, S., D. Hui, and Y. Luo (2001), Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis, *Ecol. Appl.*, *11*(5), 1349–1365.

Wang, C., B. Bond-Lamberty, and S. T. Gower (2003), Carbon distribution of a well- and poorly-drained black spruce fire chronosequence, *Global Change Biol.*, *9*, 1–14.

White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani (2000), Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: Net primary production controls, *Earth Interact.*, *4*, 1–85.

Williams, T. G., and L. B. Flanagan (1998), Measuring and modeling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*, *Plant Cell Environ.*, *21*, 64–555.

Wirth, C., E.-D. Schulze, B. Lühker, S. Grigoriev, M. Siry, G. Hardes, W. Ziegler, M. Backor, G. A. Bauer, and N. N. Vygodskaya (2002), Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests, *Plant Soil*, *242*(1), 41–63.

Zackrisson, O., T. H. DeLuca, M.-C. Nilsson, A. Sellstedt, and L. M. Berglund (2004), Nitrogen fixation increases with successional age in boreal forests, *Ecology*, *85*(12), 3327–3334.

Zhang, Y., C. Li, C. C. Trettin, H. Li, and G. Sun (2002), An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems, *Global Biogeochem. Cycles*, *16*(4), 1061, doi:10.1029/2001GB001838.

Zhuang, Q., A. D. McGuire, K. P. O'Neill, J. W. Harden, V. E. Romanovsky, and J. Yarie (2003), Modeling soil thermal and carbon dynamics of a fire chronosequence in interior Alaska, *J. Geophys. Res.*, *107*, 8147, doi:10.1029/2001JD001244. [printed *108*(D1), 2003].

B. Bond-Lamberty and S. T. Gower, Department of Forest Ecology and Management, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, USA. (bpbond@wisc.edu)

M. L. Goulden and A. McMillan, Earth System Science and Ecology and Evolutionary Biology, 3319 Croul Hall, University of California, Irvine, CA 92697, USA.