Reimplementation of the Biome-BGC model to simulate successional change

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Summary Biogeochemical process models are increasingly employed to simulate current and future forest dynamics, but most simulate only a single canopy type. This limitation means that mixed stands, canopy succession and understory dynamics cannot be modeled, severe handicaps in many forests. The goals of this study were to develop a version of Biome-BGC that supported multiple, interacting vegetation types, and to assess its performance and limitations by comparing modeled results to published data from a 150-year boreal black spruce (*Picea mariana* (Mill.) BSP) chronosequence in northern Manitoba, Canada. Model data structures and logic were modified to support an arbitrary number of interacting vegetation types; an explicit height calculation was necessary to prioritize radiation and precipitation interception. Two vegetation types, evergreen needle-leaf and deciduous broadleaf, were modeled based on site-specific meteorological and physiological data. The new version of Biome-BGC reliably simulated observed changes in leaf area, net primary production and carbon stocks, and should be useful for modeling the dynamics of mixed-species stands and ecological succession. We discuss the strengths and limitations of Biome-BGC for this application, and note areas in which further work is necessary for reliable simulation of boreal biogeochemical cycling at a landscape scale.

Keywords: black spruce, boreal forest, carbon, ecological modeling.

Introduction

Field measurements and simulation modeling are complementary, necessary approaches to studying ecosystem dynamics. This is particularly true given the mismatch between the slow rate of ecosystem change and the brevity of most research projects (Powers and Van Cleve 1991, Grace 2004). The key descriptors of forest and other terrestrial ecosystems—notably autotrophic net primary production (NPP) and net ecosystem production (NEP) or exchange (NEE)—can be laborious, destructive, time-consuming and expensive to measure (Wofsy et al. 1993, Clark et al. 2001, Gower et al. 2001, Randerson et al.

2002). Ecophysiological process models, running on increasingly cheap and powerful computers, estimate NPP and NEE by simulating processes such as photosynthesis, respiration, nutrient and water cycling, growth and mortality, and decomposition. Such models permit estimates of these processes at landscape to global scales, at which field sampling is impractical, and can simulate ecosystem responses to future climate change (Waring and Running 1998).

Biome-BGC is a non-spatial biogeochemical and ecophysiological model that uses daily meteorological data and general stand soil information, to simulate energy, carbon (C), water and nitrogen (N) cycling (Running and Coughlin 1988, Running and Hunt 1993, Thornton 1998, White et al. 2000). Leaf area index controls radiation absorption and a Farquhar photosynthesis model for a homogeneous canopy separated into sunlit and shaded leaves (Kimball et al. 1997*a*). Respiration components (heterotrophic and autotrophic growth, and autotrophic maintenance) are treated separately, and governed by Q_{10} response values. Net primary production is partitioned into biomass compartments following dynamic allocation patterns that reflect nitrogen limitations. We do not describe further the inner processes and logic of Biome-BGC, because they have been discussed in detail (Running and Coughlin 1988, Running and Gower 1991, Kimball et al. 1997*a*, Thornton 1998). The model's parameter sensitivities and other characteristics have also been analyzed extensively (White et al. 2000, Amthor et al. 2001, Potter et al. 2001, Thornton et al. 2002).

The current version (4.1.2) of Biome-BGC operates on a single vegetation type; here, vegetation type refers to a particular set of the ecophysiological parameters used by Biome-BGC to simulate biota biogeochemical cycling. These vegetation types are intended to represent coarse distinctions between functional groups, e.g., evergreen needle-leaf and deciduous broadleaf C_3 woody plants, rather than species-specific distinctions (Running and Coughlin 1988). The treatment of the ecosystem as a single canopy is a powerful simplification but poses several problems. First, mixed-species systems cannot be modeled. Forest models have traditionally focused

on even-aged single-species stands (Porté and Bartelink 2002), but most forests are heterogeneous in age and species (Landsberg and Gower 1997). Second, understory and overstory processes cannot be distinguished. This is problematic when modeling systems where the understory or ground cover plays an important role in biogeochemical cycles. For example, in the boreal forest, bryophytes sequester a large amount of carbon and form a crucial part of the water and nitrogen cycles, yet their presence, abundance and species mix depend on the overstory leaf area index (Vogel and Gower 1998, Swanson and Flanagan 2001, O'Connell et al. 2003, Turetsky 2003, Bond-Lamberty et al. 2004*b*). Third, stand succession cannot be modeled using a single vegetation type as in Biome-BGC Version 4.1.2, because the definition of succession involves replacement of one vegetation type with another (Waring and Schlesinger 1985). Such succession is an important process in most terrestrial ecosystems, and limits the temporal utility of Biome-BGC.

The goals of this study were to: (1) develop a version of Biome-BGC that supports multiple, interacting vegetation types; and (2) assess the performance and limitations of this extension to Biome-BGC by comparing the model's results to field data from multiple studies and results from the unmodified single-vegetation model. We focus here on field data, particularly published stand structural characteristics and carbon fluxes, from a 150-year boreal chronosequence in northern Manitoba, Canada.

Materials and methods

Constraint on changes to Biome-BGC

We imposed an important constraint on structural and functional changes to Biome-BGC: running the new (modified) version, hereafter termed Biome-BGC-MV, with a single vegetation type had to produce results completely identical to the 4.1.2 version. This simplified assessment of the effects of adding multiple vegetation types, and comparison with published single-vegetation results using the older model.

Structural changes to Biome-BGC

The source code of Biome-BGC Version 4.1.2 was modified to allow for multiple concurrent vegetation types. The model's internal data structures were divided into two groups: those that tracked only site variables (e.g., meteorological data, soil carbon and nitrogen pools), and thus required no modification; and those that tracked vegetation-specific variables (e.g., vegetation pools and fluxes). Leaf litter, woody litter and coarse woody debris were considered specific to a particular vegetation type until entering soil pools via decomposition. For example, Figure 1 shows the division between site- and vegetation-specific variables for the model's internal nitrogen cycle. Internally, the static data structures tracking vegetation-specific information were replaced by pointers to arrays of such structures; the only limit to the number of vegetation types the model can track are the computational resources. For more details, see the Appendix and the Biome-BGC source code; this
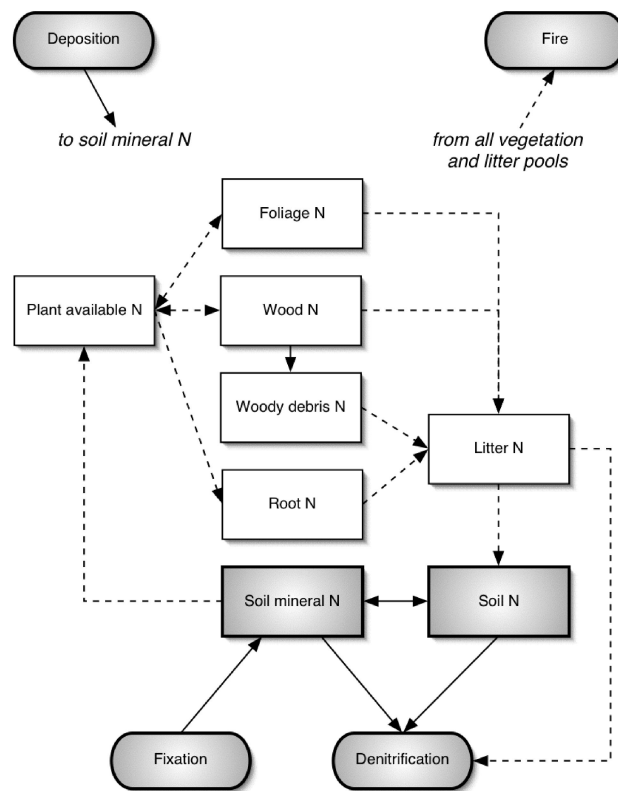

Figure 1. Simplified schematic of nitrogen (N) cycling in Biome-BGC, showing pools and fluxes. Ovals represent ecosystem sources or sinks. Pools and fluxes were categorized as vegetation- (light boxes and dashed lines) or site-specific (dark boxes and solid lines).

code has extensive internal documentation and is available from the Numerical Terradynamic Simulation Group at the School of Forestry, University of Montana (http://www.ntsg. umt.edu).

Input and output of the modified model function largely as in the 4.1.2 version. Instead of reading a single set of ecophysiological constants (EPC), Biome-BGC-MV reads the number of vegetation types to model and then a list of EPC files. These EPC files are identical to the older-version files except for two extra parameters, discussed below. Initial C and N values for leaves, wood, litter, and woody debris are specified on a vegetation-specific, not a site-specific, basis. There is no change in how output variables are specified, but variables are tracked and written on a vegetation-specific basis. Site-level variables (e.g., NEP or soil respiration) can of course still be output.

Functional changes to Biome-BGC

Many Biome-BGC processes required few changes or none. For example, modeled N deposition, snow melt and water outflow do not directly depend on vegetation, and operate as in version 4.1.2. Conversely, photosynthesis, carbon allocation and respiration are vegetation-specific processes, and in Biome-BGC-MV, are computed separately on the vegetation-specific data structures. Similarly, daily updating of state vari-

ables is done separately for each vegetation type, and once for non-vegetation-specific (primarily soil) pools. More fundamental modifications were required in areas where vegetation types compete for resources. The implementation of competition between vegetation types for light and precipitation interception was based on vegetation height. Two EPC parameters were added to describe the relationship between mass (m; kg C m^{-2}) and height (h; m) for each vegetation type. An exponential equation of the form:

$$h = h_{max}(1 - e^{-\frac{5}{m_{hmax}}m})\qquad(1)$$

was chosen to describe this relationship. The two parameters supplied for each vegetation type are h_{max}, the maximum vegetation height, and m_{hmax}, the vegetation mass at which this height is attained. This equation form has the advantage that both parameters have easily understandable meanings (in contrast, for example, to a polynomial equation) (Bates and Watts 1988). The constant value of 5 in Equation 1 ensures that h will rise to within 1% of h_{max} by $m = m_{max}$. At the beginning of each simulation year, Biome-BGC-MV computes the height of each vegetation type based on current stem (for woody plants) or leaf (for nonwoody plants) mass. All light and precipitation interception for the subsequent year occurs using this height order, with the tallest vegetation intercepting first; light or precipitation that is not intercepted becoming available to the next tallest vegetation type. The height order is not currently used by any other process.

Competition among plants for N and soil water is more complex and less well understood than for light (Lambers et al. 1998), and the existing Biome-BGC logic regarding these processes was not changed. For N, total demand from plant uptake, litter decomposition and soil processes is assessed; if demand is greater than the available soil mineral N pool, every potential demand flux (calculated beforehand, based on vegetation type growth and soil decomposition potential) is reduced by the same proportion, such that all available N will be used. 'Spinup' mode, where extra N is added to the system to satisfy a portion of total demand, was unchanged. A similar logic is followed for soil water uptake. In Biome-BGC-MV, as in the 4.1.2 version, plants receive no benefit in N or water uptake from photosynthate investment in fine roots (White et al. 2000), with plant uptake treated as a function only of demand versus supply (Thornton 1998). The Appendix highlights major changes in internal model logic.

Comparison with field chronosequence data

Results of the modified Biome-BGC model were compared with data from a well-drained black spruce (*Picea mariana* (Mill.) BSP)-dominated fire chronosequence west of Thompson, Manitoba, Canada, near the BOREAS Northern Study Area (55°53′ N, 98°20′ W). The chronosequence consisted of seven different-aged black spruce forests; the oldest stand in the chronoseqence (151 years) was the BOREAS NSA tower site (Sellers et al. 1997, Goulden et al. 1998). The stands have been studied extensively, and differed in their species mix

(Bond-Lamberty et al. 2002*b*, Wang et al. 2003), leaf area (Bond-Lamberty et al. 2002*b*), soil and woody debris CO_2 fluxes (Bond-Lamberty et al. 2002*a*, Wang et al. 2002*b*), carbon distribution (Wang et al. 2003), net primary production and net ecosystem production (Bond-Lamberty et al. 2004*b*), heterotrophic soil respiration (Bond-Lamberty et al. 2004*a*) and net ecosystem exchange (Litvak et al. 2002). The stands were dominated by three tree species: trembling aspen (*Populus tremuloides* Michx), black spruce, and to a lesser extent jack pine (*Pinus banksiana* Lamb.). Early successional deciduous tree species give way to black spruce in the older chronosequence 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.). The chronosequence was unreplicated, but (1) its understory and overstory succession patterns were similar to those seen in other studies of boreal black spruce (Black and Bliss 1978, Foster 1985); and (2) it was found to be representative of an additional 14 stands sampled in the 500 × 500 km BOREAS northern study area (Bond-Lamberty et al. 2004*b*).

Model data sources: site, soil and meteorological parameters

All parameters needed to reproduce the results reported below are given in Tables 1 and 2, except for the daily meteorological data, for which summaries are presented. Site-specific parameters (Table 1) used to model the black spruce chronosequence generally follow the values given by Amthor et al. (2001) and Kimball et al. (1997*a*). Effective soil depth was set to 0.5 m, following those authors. Atmospheric CO_2 concentration was treated as a constant 320 ppm, approximately the historical value 'halfway' through the chronosequence (i.e., about 1930) (IPCC 2001).

The primary source of meteorological data was the regional and global coverage of meteorological parameters available from the NCEP/NCAR Reanalysis Project (Kalnay et al. 1996, Kistler et al. 2001). These data span the period from 1948 to the present with a global grid resolution of 192 × 94 (~2°); only 20 years (1980–1999) were used for the BOREAS region simulated here. Two supplementary datasets were used as checks on the applicability of the NCEP/NCAR data: (1) the site-specific surface meteorological and radiation parameters collected during BOREAS (Osborne et al. 1998); and (2) each chronosequence stand was instrumented for four years (1999–2003) with micrometeorological stations recording air and soil temperatures, photosynthetically active radiation (PAR), relative humidity and soil water content. These data were used to verify that the NCEP/NCAR data accurately represented local conditions.

We used monthly precipitation data from the Global Precipitation Climatology Project (GPCP) (Adler et al. 2003). Grid size for these data is 144 × 72 cells, with a spatial resolution of 2.5°. To apportion these values into the daily time step required by Biome-BGC, we used the precipitation interval (i.e., days between precipitation events) recorded by the on-site micrometeorological stations noted previously; these precipitation patterns generally matched data recorded at the BOR-

Table 1. Simulation site parameters for the black spruce chronosequence in BOREAS NSA. Meteorological data summarize the climate file that drove the simulation, and are given as annual means ± 1 SD (based on 20 years of daily data; see text).

Parameter	Value	Reference
Site and soil		
Elevation (m)	260	Halliwell and Apps (1997)
Latitude (°)	55.9	Halliwell and Apps (1997)
Albedo (%)	10.0	Betts and Ball (1997)
Effective soil depth (m)	0.5	Steele et al. (1997)
Sand:silt:clay ratio	26:29:45	Burke et al. (1997)
Nitrogen deposition ($kg\ N\ m^{-2}\ year^{-1}$)	0.0004	Peng and Apps (1998)
Nitrogen fixation ($kg\ N\ m^{-2}\ year^{-1}$)	0.0006	Peng and Apps (1998)
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	

EAS NSA flux tower and available through the ORNL/DAAC and Ameriflux web sites. These observed data (mean monthly precipitation intervals of 15, 12, 15, 3, 3, 2, 2, 2, 2, 3, 9 and 16 days for January to December, respectively) were used to "space" the monthly NCEP/NCAR precipitation data to daily values.

Model data sources: plant ecophysiological parameters

Two tree vegetation types were simulated, evergreen needle-leaf (primarily *P. mariana* in the chronosequence) and broadleaf deciduous (primarily *P. tremuloides*). Plant ecophysiological parameters are summarized in Table 2. We used the same or similar values as those given by Kimball et al. (1997*a*, 1997*b*, 2000), except in the following cases when site-specific data were available. Annual fire mortality was set to zero, because this simulation was designed to replicate 150 years of fire-free growth in these stands, and was not concerned with fire losses at larger temporal or spatial scales. Fine root turnover was set to 1.0 year^{-1}, the default behavior of Biome-BGC 4.1.2. Nitrogen concentrations, and thus C:N ratios of stem wood, foliage and leaf litter, were taken from Gower et al. (2000) as well as from the chronosequence sites (Bond-Lamberty, unpublished data). The days of the year on which to start new growth and end litterfall, not shown in Table 2, were automatically calculated by Biome-GC.

The two new parameters that defined the mass-to-height relationship for each vegetation type (Table 2) were computed from data given by Wang et al. (2003) for *P. mariana* ($n = 24$,

$r^2 = 0.98$) and J. Martin (University of Wisconsin, Madison, WI, unpublished data) for *P. tremuloides* ($n = 13$, $r^2 = 0.37$). The *P. mariana* data were from the chronosequence described and the *P. tremuloides* data were collected in aspen-dominated boreal forests 100 km to the south.

Model data sources: initial site C and N pools

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. Coarse woody debris values for the evergreen needle-leaf and deciduous broadleaf vegetation types were set to 4.7 and 0.0 kg C m^{-2}, respectively (Bond-Lamberty et al. 2002*a*, Wang et al. 2003); the latter value was zero because mature black spruce stands are single-species stands after canopy closure at 50–60 years (Black and Bliss 1978, Bond-Lamberty et al. 2002*b*, Wang et al. 2003). All fine litter C and N values, as well as soil mineral N (which differs from total soil N; cf. Figure 1), were set to 0.0 kg m^{-2}, assuming complete volatilization in fire (Stocks and Kauffman 1997, Wang et al. 2003). 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 that used by Kimball et al. (1997*a*, 2000).

Single-vegetation simulation and ensembling

All simulations were performed with Biome-BGC-MV, the modified multi-vegetation Biome-BGC. For comparison, single-vegetation simulations were also performed with the evergreen needle-leaf and deciduous broadleaf parameters given in Table 2; as noted previously, these results were identical to results obtained with the current 4.1.2 version of the model. For all simulations, we used the ensembling method of Thornton et al. (2002) to remove the effects of interannual climate variability from the modeled results. The ensembling method factors out the relative timing of disturbance vis-à-vis climate variation by taking the mean of 20 simulations, with each simulation commencing at a different year in the meteorological data file. The results presented here thus represent the mean of an ensemble of model simulations.

Results

Computational speed of the new model

When simulating one and two vegetation types, Biome-BGC-MV execution required approximately 110 and 190%, respectively, of the time required by the single-vegetation 4.1.2 version. A test run with three vegetation types, not discussed further here, required 260% of the original version's execution time.

Net primary production, leaf area index and stem mass

Biome-BGC-MV simulated NPP of deciduous broadleaf trees reasonably well across the chronosequence (Figure 2). Simulated evergreen needle-leaf NPP matched the field data well for the two oldest and three youngest chronosequence stands, but was significantly lower than measured NPP in the 19- and 37-year-old stands. The single-vegetation evergreen needle-

Table 2. Simulation ecophysiological parameters by vegetation type (evergreen needle-leaf (ENL) and deciduous broadleaf (DBL)). Where no reference is given, the value listed is the default value distributed with Biome-BGC. Abbreviations: C = carbon; N = nitrogen; LAI= leaf area index; SLA = specific leaf area; g_s = stomatal conductance; Ψ_L = leaf water potential; and VPD = vapor pressure deficit.

Parameter	ENL	DBL	Reference
Phenology and turnover			
Transfer growth period (% growing season)	30	20	
Litterfall period (% growing season)	30	20	
Leaf turnover (year^{-1})	0.12	1.0	Bond-Lamberty et al. (2004*b*), Gower et al. (1997), Steele et al. (1997)
Live wood turnover (year^{-1})	0.7	0.7	
Whole-plant mortality (year^{-1})	0.01	0.01	Bond-Lamberty et al. (2004*b*)
Fire mortality (year^{-1})	0.0	0.0	See text
Allocation and N requirements			
Fine root C:leaf C	1.6	1.5	Bond-Lamberty et al. (2004*b*)
Stem C:leaf C	2.3	2.0	Bond-Lamberty et al. (2004*b*)
Live wood C:total wood C	0.1	0.1	
Coarse root C:stem C	0.3	0.4	Bond-Lamberty et al. (2004*b*)
Growth C:storage C	0.5	0.5	
Leaf C:leaf N	59.6	19.8	Gower et al. (1997, 2000)
Leaf litter C:leaf litter N	90.0	34.6	Gower et al. (1997, 2000)
Fine root C:fine root N	60.0	19.8	Gower et al. (1997, 2000)
Live wood C:live wood N	151.5	92.6	Gower et al. (1997, 2000)
Dead wood C:dead wood N	714.3	625.0	Gower et al. (1997, 2000)
Leaf litter labile:cellulose:lignin (%)	32:44:24	39:44:17	
Fine root labile:cellulose:lignin (%)	30:45:25	30:45:25	
Dead wood cellulose:lignin (%)	76:24	76:24	
Canopy parameters			
Water interception (LAI^{-1} day^{-1})	0.01	0.01	
Light extinction	−0.5	−0.5	
SLA (projected area basis) (m^2 kg^{-1} C)	8.3	38.7	Bond-Lamberty et al. (2002*b*)
Shaded/sunlit SLA	2.0	2.0	
All sided:projected leaf area	3.1	2.0	Bond-Lamberty et al. (2003)
Maximum vegetation height (m)	15.8	13.2	See text
Mass at maximum height (kg C m^{-2})	12.0	12.5	See text
Leaf N in Rubisco (%)	6.0	14.0	Field and Mooney (1986), Fan et al. (1995)
Maximum g_s (mm s^{-1})	3.0	5.0	Nobel (1991), B.E. Ewers (University of Wyoming, unpublished data)
Cuticular conductance (mm s^{-1})	0.01	0.01	Kimball et al. (1997*a*) Nobel (1991)
Boundary layer conductance (mm s^{-1})	80.0	20.0	Nobel (1991), B.E. Ewers (University of Wyoming, unpublished data)
Ψ_L start of g_s reduction (MPa)	−0.5	−0.5	Kimball et al. (1997*a*), Nobel (1991)
Ψ_L complete g_s reduction (MPa)	−1.7	−2.3	Kimball et al. (1997*a*), Nobel (1991)
VPD start of g_s reduction (kPa)	1.0	1.0	Kimball et al. (1997*a*), Nobel (1991)
VPD complete g_s reduction (kPa)	4.1	4.0	Kimball et al. (1997*a*), Nobel (1991)

leaf simulation (here termed ENL-1, Figure 2) simulated (correctly) high NPP in the 19-year-old stand before declining, by 150 years after wildfire, to a value similar to that of evergreen needle-leaf in the multi-vegetation simulation. The single-vegetation deciduous broadleaf simulation (DBL-1, not shown) was similar to ENL-1, with high (200–300 g C m^{-2} year^{-1}) NPP 10–15 years after wildfire, declining thereafter.

Biome-BGC-MV simulated leaf area index (LAI) well for both vegetation types (Figure 3), although deciduous broadleaf LAI was somewhat higher than measured values in the youngest stands. The ENL-1 and DBL-1 simulations reached high LAI values (5–6) by 20 years after wildfire, far too early

based on comparison with the measured field data, before declining. Biome-BGC-MV generally under-predicted evergreen needle-leaf stem mass and over-predicted deciduous broadleaf stem mass (Figure 4), although the values for the oldest stands were close to observed values. Both ENL-1 and DBL-1 (not shown, but similar to ENL-1 shown) simulated stem mass values that were far higher than observed values, particularly in the younger stands.

Growth limitations from light, nitrogen, water and VPD

The Biome-BGC-MV simulation became increasingly N-deficient over time: in the oldest stands, N supply was less than
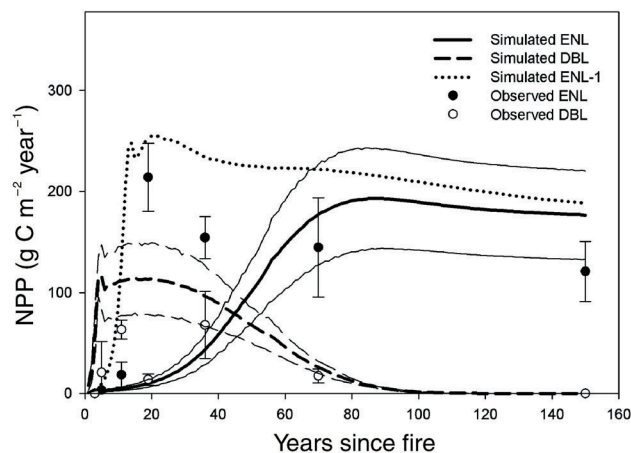
Figure 2. Comparison of simulated and observed net primary production (NPP) across the chronosequence, for evergreen needle-leaf (ENL) and deciduous broadleaf (DBL) vegetation types. Thin lines bracketing main ENL and DBL lines show standard deviations of ensembling procedure (i.e., show effect of interannual meteorological variability; see text). Results of a single-vegetation ENL simulation (ENL-1) are also shown. Observed data are from the well-drained black spruce chronosequence discussed by Bond-Lamberty et al. (2004*b*). Error bars show plot-to-plot standard deviation ($n = 4$).

Figure 3. Comparison of simulated and observed leaf area index (LAI) across the chronosequence, by vegetation type. Biome-BGC LAI output was converted to the standard $m^2 m^{-2}$, displayed, based on a carbon to biomass ratio of 0.45 (Atjay et al. 1977). Observed data are from Bond-Lamberty et al. (2002*b*).

half of the combined demand of vegetation and decomposition processes (Figure 5a). After removing meteorological variability, the effects of leaf water potential (Ψ_L) and atmospheric vapor pressure deficit (VPD) on stomatal conductance were almost constant (Figures 5b and 5c), with the evergreen needle-leaf vegetation type slightly more sensitive to Ψ_L and the deciduous broadleaf vegetation type slightly more sensitive to VPD (as specified in the initial parameters, Table 2). A noticeable improvement in the latter occurred when the deciduous broadleaf vegetation type was overtopped by the evergreen needle-leaf vegetation type. This overtopping had a marked effect on deciduous broadleaf shortwave interception, which dipped suddenly 50–60 years after fire (Figure 5d).
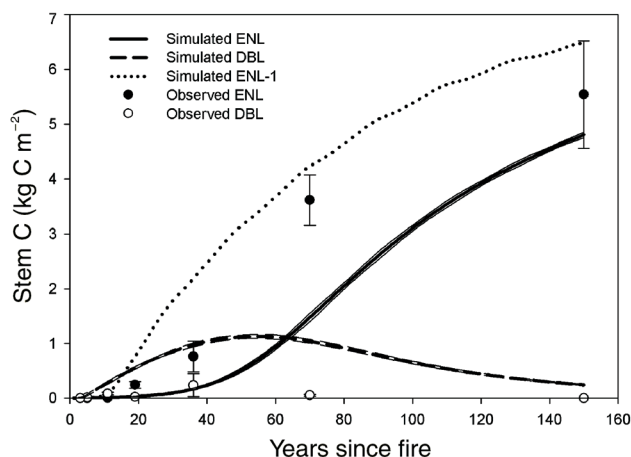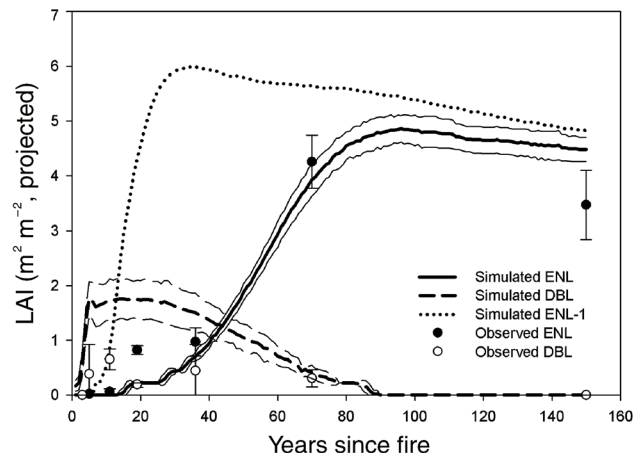

Figure 4. Comparison of simulated and observed stem carbon (C) across the chronosequence, by vegetation type. Observed data are from Wang et al. (2003).
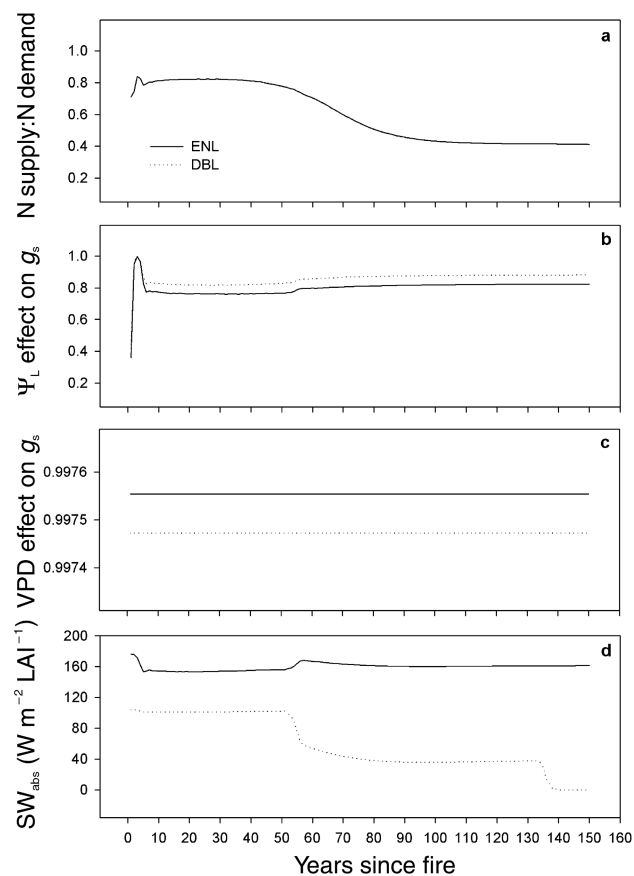

Figure 5. (a) Nitrogen (N) shortfall, computed as mineral N supply divided by total demand; (b) leaf water potential (Ψ_L) effect on stomatal conductance (g_s), where 1.0 is no effect and 0.0 is full stomatal closure; (c) vapor pressure deficit (VPD) effect on g_s, where 1.0 is no effect and 0.0 is full stomatal closure; and (d) absorbed shortwave radiation per unit projected leaf area (SW_{abs}). Figures show mean of daily values for each simulation year, for evergreen needle-leaf (ENL) and deciduous broadleaf (DBL) vegetation types. The ENL and DBL values overlap in (a).

Discussion

Comparing a simulation and a chronosequence

The chronosequence used in the simulation comparisons presented here has been shown to be representative of a large group of regional stands (Bond-Lamberty et al. 2004*b*), but there is no guarantee that any process model—however perfectly parameterized, flawless its internal logic or exact the field measurements to which it is compared—could replicate each chronosequence member correctly; even if it did, this would not 'verify' the model (Oreskes et al. 1994). In addition, species' successional patterns tend to be relatively variable in younger stands (Landsberg and Gower 1997). Thus, this discussion focuses less on why particular stands in the chronosequence were 'missed' than on the broader trends, sensitivities, strengths and limitations of Biome-BGC.

Model parameterization

The Biome-BGC model family has known parameter sensitivities, most notably to stomatal conductance, allocation ratios, C:N ratios and leaf turnover (White et al. 2000, Potter et al. 2001). Precipitation and soil water had strong effects on both NPP and species composition, yet the dynamics of soil water evaporation and drainage in the model differed considerably from those in the field; this point is discussed further below. Nitrogen fixation was treated as a constant low value (Table 1), but almost certainly varied across the chronosequence, because several boreal understory and moss species are known to symbiotically fix N (Mäkipää 1995, Vogel and Gower 1998, DeLuca et al. 2002, Turetsky 2003). Green alder (*Alnus crispa* (Ait.) Pursh), for example, was present in the 70-year-old stand (Bond-Lamberty et al. 2002*b*), but unaccounted for in our simulation. The presence of *Alnus* can strongly affect boreal forest growth (Vogel and Gower 1998, Gower et al. 2000), and its absence from the simulation may provide a partial explanation for why Biome-BGC-MV could not replicate the high evergreen needle-leaf stem mass observed in this stand (Figure 4).

More generally, many ecophysiological properties are fixed at the beginning of a simulation in Biome-BGC (cf. Table 2). In the real world, however, these values frequently change with stand age; e.g., specific leaf area (Hager and Sterba 1985, Bond-Lamberty et al. 2002*b*), leaf geometry (Bond-Lamberty et al. 2003), hydraulic characteristics (Ewers et al. 2000, McDowell et al. 2002) or photosynthate allocation (Gower et al. 1994, Law et al. 2001, Bond-Lamberty et al. 2004*b*). We generally chose to parameterize the model based on values from the oldest chronosequence stands, in particular the NOBS tower site, which is well studied and had been modeled previously with Biome-BGC (Kimball et al. 1997*a*, 1997*b*, Amthor et al. 2001). This biased parameterization may be one reason, along with chronosequence artefacts and successional variability noted previously, why the model did not perform as well at the younger stands as at the older stands. Similarly, our model results include only two overstory tree types, evergreen needle-leaf and deciduous broadleaf. This is a reasonable sim-

plification for the older chronosequence stands (Wang et al. 2003), but the younger stands are much more diverse in their species mix, and have a highly productive (100–150 g C m^{-2} year^{-1} or 40–100% of total NPP) understory (Bond-Lamberty et al. 2004*b*) that was unaccounted for in our model. Some of this production is subsumed in the evergreen needle-leaf and deciduous broadleaf results, in the sense that young overstory trees face more competition for resources in the field than simulated here.

Species succession

Most simulation studies of the Canadian boreal forest using process models have focused on mature stands of single species (Peng et al. 1998, Liu et al. 1999, Peng and Apps 1999, Price et al. 1999, Amthor et al. 2001, Wang et al. 2002*c*). Even when younger stands or stand development is considered, species succession is generally ignored (Keyser et al. 2000, Zhuang et al. 2003, Thornley and Cannell 2004). Biome-BGC was not originally designed to simulate species succession. Nonetheless, the simulated transition from deciduous broadleaf to evergreen needle-leaf overstory dominance (55–60 years after fire) matched field results well (Bond-Lamberty et al. 2002*b*, Wang et al. 2003). The deciduous broadleaf decline was driven by several factors. Low temperatures and long winters (Table 1) increase the advantage of an evergreen leaf habit, because deciduous plants have a shorter growing season in which to accumulate carbon (Fan et al. 1995, Baldocchi and Vogel 1996, Black et al. 1996, Linder et al. 1997). The simulated system was quite N-deficient (Figure 5a), as are many boreal forests (Linder et al. 1987, Schimel et al. 1996), increasing the cost of building an N-rich (Table 2) broadleaf canopy. Low soil water frequently constrained stomatal conductance during the growing season, again increasing the advantage of an evergreen needle-leaf habit.

Once the height of the evergreen needle-leaf vegetation type exceeded that of the deciduous broadleaf vegetation type, available radiation dropped abruptly in the broadleaf vegetation type (Figure 5d). Such an abrupt transition may be unrealistic, and we acknowledge that the entire mechanism of converting stem biomass per unit area to vegetation height is simplistic (Landsberg and Gower 1997); it also has the disconcerting effect of "shrinking" the deciduous broadleaf canopy as its stem mass declines in the middle of the chronosequence (Figure 4). Given the non-spatial nature of Biome-BGC (i.e., in the model, vegetation mass is expressed as kg C m^{-2}, but no stocking or density information is tracked), and the need to prioritize radiation and precipitation interception, a mass-to-height conversion is necessary, albeit crude.

Medium- and long-term carbon dynamics

Biome-BGC has been extensively tested for simulating boreal forest carbon and hydrologic dynamics on the daily to annual timescale (Kimball et al. 1997*a*, 1997*b*, Amthor et al. 2001). There have been fewer medium-term applications, i.e., on the decade to century scale (Keyser et al. 2000, Law et al. 2001). In our study, Biome-BGC-MV was generally able to repro-

duce tree NPP, leaf area and stem mass for a seven-stand, 150-year chronosequence, for both evergreen needle-leaf and deciduous broadleaf vegetation types. We can thus answer affirmatively the question posed by Amthor et al. (2001): Biome-BGC can, when initialized to a burned black spruce forest and run for 150 years, generate a forest with the same characteristics as the present NSA-OBS (150-year-old) site (Gower et al. 1997, Sellers et al. 1997). The single- and multi-vegetation simulations had similar values for NPP, LAI and stem C after 151 years, but significantly different dynamics in the younger stands. We conclude that accurately simulating these variables over stand development based on a single vegetation type is unrealistic.

Challenges in using Biome-BGC to model boreal forest biogeochemical cycling

Forest ecosystem modelers must choose how to simplify and internally represent the real-world system under study, and their choices constrain subsequent model use (Jackson et al. 2000, Porté and Bartelink 2002). Process-based models such as Biome-BGC offer advantages over inventory- or transition-based models (Li et al. 2002, Yemshanov and Perera 2002) in simulating boreal forest dynamics, particularly responses to future climate and disturbance conditions (Bonan 1989, Peng and Apps 1999, Wang et al. 2002c, Yarie and Billings 2002). Nonetheless, several characteristics of Biome-BGC pose challenges in robustly modeling boreal forests across time and space.

Biome-BGC has no provision for the mechanistic simulation of nonvascular plants, a trait it shares with several other models used to model boreal forests (Peng and Apps 1999, Yarie and Billings 2002, Zhuang et al. 2003, Thornley and Cannell 2004). This is a particular problem in the boreal forest, where bryophytes constitute an important, and often dominant, part of C and N cycles (Camill et al. 2001, O'Connell et al. 2003, Bond-Lamberty et al. 2004b). Bryophytes have no roots or stomates; they heavily insulate the soil beneath them; and their litter lacks lignin yet is highly resistant to decay (Turetsky 2003). These characteristics differ significantly from the Biome-BGC ecophysiological model. It is not clear if the existing photosynthesis, allocation, growth and decay logic can be used to approximate bryophyte dynamics, or if entirely new model logic would be necessary.

Soil temperature (T_{soil}) presents a further difficulty. The large amount of C stored in boreal soils, and the dependence of respiration on temperature, mean that T_{soil} plays an important role in boreal simulations. Its simulation may be more problematic in these systems (Zhuang et al. 2003) because of the insulating effects of bryophytes, poor soil drainage and high LAI (O'Neill et al. 2002, Wang et al. 2002a), factors that are frequently correlated (Harden et al. 1997, Bisbee et al. 2001). For example, Biome-BGC uses soil temperature at 10-cm depth (T_{10}) as a driver for autotrophic and heterotrophic below-ground respiration. Comparing Biome-BGC's simulated T_{10} with observed values from the chronosequence, we note that simulated T_{10} tracks observed T_{10} for the 12-year-old chrono-
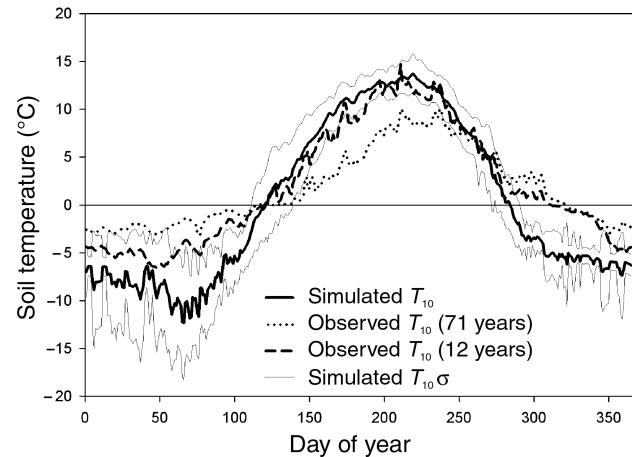

Figure 6. Mean soil temperature at 10 cm (T_{10}) as simulated by Biome-BGC (with error lines showing the effect of interannual variability, $n = 20$ years) compared with mean observed T_{10} ($n = 4$ years). Data from two chronosequence stands, similar in drainage and aspect, are shown: a 12-year-old stand with an open canopy and no moss cover, and a 71-year-old stand with continuous feathermoss cover and a closed *Picea mariana* canopy.

sequence stand, with its open canopy and lack of moss, reasonably well (Figure 6). Observed soil T_{10} at an older stand, which is similar in most respects such as slope, aspect and drainage to the younger stand, diverges significantly from the simulated value; this difference, in particular the relatively low temperatures observed in the first part of the growing season, is probably a result of the thick feathermoss ground cover (Wang et al. 2003), closed canopy and high LAI (Bond-Lamberty et al. 2002b) of the site. Thus insulating effects on soil temperature need to be considered.

Finally, in much of the Canadian boreal forest, well-drained areas are the exception, not the rule (National Wetlands Working Group 1988). Poorly drained areas often have high rates of NPP and NEP (Harden et al. 1997, Camill et al. 2001, Vitt et al. 2001, Bond-Lamberty et al. 2004b), low decomposition rates and different successional pathways (Foster 1985, Wang et al. 2003). Currently in Biome-BGC, soil water outflow always occurs if soil water exceeds field capacity, and tree growth is unaffected by excessive soil water; both of these behaviors are problematic. Pietsch et al. (2003) extended Biome-BGC to account for seasonal flooding and groundwater infiltration. Their logic is complex but accounts for extra N deposition as a result of floodwater, as well as the effects of gravitation and soil matric water potential. For many applications, a much simpler mechanism—restricting outflow on a site-specific basis, for example—might be adequate, and should be explored.

Conclusions

The modified Biome-BGC is able to model multiple interacting and competing vegetation types at a single site, and thus is able to track forest succession through time. Although Biome-BGC was not originally designed to simulate vegetation com-

petition, it reliably simulated changes in various biogeochemical cycling components (particularly leaf habit, NPP, C stocks and transpiration) seen in a boreal black spruce chronosequence. Further work is necessary to develop reliable simulations of boreal biogeochemical cycling at the landscape scale, but this new version should be useful for researchers interested in modeling longer-term and more complex forest dynamics than were previously possible with Biome-BGC.

Acknowledgments

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Appendix

Table A1. Summary list of the internal Biome-BGC routines whose logic was fundamentally changed in the implementation of the multiple vegetation types ("vegtypes") version Biome-BGC-MV. The list will be of most use when working with the model source code. This code, with a user's guide and extensive internal documentation, is available from the Numerical Terradynamic Simulation Group at the School of Forestry, University of Montana (http://www.ntsg.umt.edu).

Function name	Purpose	Description of changes
bgc() and *spinup_bgc()*	Core model logic	These two functions combined into a single function; structure of main model loop depends on whether simulation is a 'normal' or 'spinup.' Competition indices—currently only vegetation height—are recalculated annually.
daily_allocation() and *spinup_daily_allocation()*	Daily allocation of C and N; reconciliation of microbial N immobilization; addition of supplemental N in spinup mode	These two functions combined into a single function whose behavior is governed by a flag. Total N demand across all vegtypes, and demand from litter and soil processes calculated in *decomp()* below, are assessed before assigning daily allocations. If there is an N shortfall, all demands are scaled back by the same percentage.
decomp()	Calculate potential decomposition fluxes	Immobilization demand calculated for each vegtype and soil processes and summed to the site level.
prcp_route()	Calculate canopy interception of precipitation	Called for each vegtype in order of height; a static variable tracks precipitation as it falls through the canopies. Each vegtype intercepts and stores water separately, and available precipitation diminishes with successive canopy intercepts.
radtrans()	Calculate canopy interception of radiation	Called for each vegtype in order of height. The shortwave flux transmitted by each canopy becomes the incoming flux for the next; each vegtype intercepts light separately and diminishes available light for subsequent canopies.