Simulating effects of fire disturbance and climate change on boreal forest productivity and evapotranspiration

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Abstract

We used a terrestrial ecosystem process model, BIOME-BGC, to investigate historical climate change and fire disturbance effects on regional carbon and water budgets within a 357,500 km² portion of the Canadian boreal forest. Historical patterns of increasing atmospheric CO₂, climate change, and regional fire activity were used as model drivers to evaluate the relative effects of these impacts to spatial patterns and temporal trends in forest net primary production (NPP) and evapotranspiration (ET). Historical trends of increasing atmospheric CO₂ resulted in overall 13% and 5% increases in annual NPP and ET from 1994 to 1996, respectively. NPP was found to be relatively sensitive to changes in air temperature (Tₐ), while ET was more sensitive to precipitation (P) change within the ranges of observed climate variability (e.g., ±2 °C for Tₐ and ±20% for P). In addition, the potential effect of climate change related warming on NPP is exacerbated or offset depending on whether these changes are accompanied by respective decreases or increases in precipitation. Historical fire activity generally resulted in reductions of both NPP and ET, which consumed an average of approximately 6% of annual NPP from 1959 to 1996. Areas currently occupied by dry conifer forests were found to be subject to more frequent fire activity, which consumed approximately 8% of annual NPP. The results of this study show that the North American boreal ecosystem is sensitive to historical patterns of increasing atmospheric CO₂, climate change and regional fire activity. The relative impacts of these disturbances on NPP and ET interact in complex ways and are spatially variable depending on regional land cover and climate gradients.

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1. Introduction

Terrestrial carbon cycles exhibit spatial and temporal variability in response to natural climatic fluctuations and environmental gradients, as well as anthropogenic and natural disturbances. The boreal forest biome is of special concern for global carbon cycle research because it contains roughly 14% of the world’s vegetation cover, and 27% and 28% of the world’s vegetation and soil carbon inventories, respectively (McGuire et al., 1995, 1997). The boreal forest is also experiencing unprecedented changes in regional climate (Barber et al., 2000; Serreze et al., 2000). Over the past 30 years annual surface air temperatures have increased by approximately 5 °C in Alaskan boreal and arctic regions (Larcher and Marshall, 1986), Canadian boreal forest (Beltrami and Mareschal, 1994), and North America in general (Oechel and Vourlitis, 1994). Consequent summer drought has reduced growth of Alaskan white spruce in the 20th century (Barber et al., 2000) with potential increases in regional fire occurrence (Wotton and Flannigan, 1993). The annual area burned has increased by an approximate factor of 3 in boreal North America from 1.2 × 10⁶ ha in the 1960s to 3.2 × 10⁶ ha in the 1990s (Zimov et al., 1999). Wildfires in boreal forests show tremendous interannual variation in both severity and area burned (Harden et al., 2000). In the 1980s in Canada, 10 times more land area was burned than in any previous decade on record (Murphy et al., 1999). Wildfires affect atmospheric CO₂ concentrations through direct
inputs from biomass burning and indirectly by altering species composition, net primary production and net carbon exchange (Zimov et al., 1999).

Net primary production (NPP) is the primary conduit of carbon transfer from the atmosphere to the land surface and is thus a fundamental component of the global carbon cycle. Long-term satellite remote sensing observations of high latitude greening indicate a regional response of increasing NPP and accelerated sequestration and storage of atmospheric CO₂ by vegetation in boreal latitudes (Myneni et al., 1997; Keyser et al., 2000; Nemani et al., 2003). Some atmospheric inversion analyses also suggest that carbon storage in North American boreal forests has been generally increasing since the early 1980s (McGuire et al., 2004; Dargaville et al., 2002). This enhanced NPP and associated storage of atmospheric CO₂ may be a direct response to longer growing seasons and more favorable temperatures for photosynthesis under a warming climate (Jarvis and Linder, 2000; Nemani et al., 2003). Increasing atmospheric CO₂ levels may also enhance NPP by stimulating canopy photosynthesis, particularly for water and N limited systems (Drake et al., 1997; Loustau et al., 2001). Other potential mechanisms favoring enhanced NPP include atmospheric nitrogen (N) deposition and warming induced increases in soil N mineralization (McGuire et al., 1992; Schimel et al., 1996). The status and relative strength of the landscape as a net source or sink for atmospheric CO₂, however, is dependent on the balance between terrestrial carbon uptake through NPP and carbon release from volatilization and respiration processes. Fire frequency across portions of the North American boreal forest has increased substantially in the late 20th century in conjunction with regional warming trends, with the potential for further increases in response to continued climate warming (Stocks et al., 2000; Podur et al., 2002). Recent increases in boreal fire activity imply a net decrease in vegetation carbon storage, though the net effect of these changes on regional NPP is uncertain.

Evapotranspiration (ET) defines the land–atmosphere exchange of water and is the primary interface between terrestrial energy and water cycles. ET is also closely linked to NPP and the carbon cycle through vegetation canopy stomatal controls for both CO₂ and water vapor (i.e., transpiration), and the effect of ET on the soil water balance which strongly influences decomposition and respiration processes. ET in boreal landscapes is relatively low compared to temperate forests due to low temperature and leaf N constraints to canopy stomatal conductance (Baldocchi et al., 2000). Recent warming trends and associated increases in terrestrial productivity in boreal regions also imply increases in ET, though the relative magnitudes of these increases and impacts from fire disturbance over large, complex boreal landscapes are uncertain.

Interactions among atmospheric CO₂ dynamics, global climate change, and increased wildfires are likely to affect boreal forest carbon sequestration and storage in a variety of ways (Peng and Apps, 1999; Chen et al., 2000). These regional disturbances are intrinsically spatially and temporally heterogeneous and likely invoke similarly complex responses in boreal forest productivity and water cycles. Current understanding of these effects is incomplete because of the potential sensitivity of the system to multiple perturbations, which are interactive in complex ways and may have non-linear impacts on regional NPP and ET. In this study, we investigated the individual and combined effects of historical patterns of increasing atmospheric CO₂ concentrations, climate change, and wildfires on spatial and temporal dynamics of boreal forest NPP and ET across a 357,500 km² portion of central Canada. We conducted a series of spatially explicit mesoscale (∼10 km spatial resolution) simulations of long-term daily carbon and water budgets across the study region using an ecosystem process model (BIOME-BGC) modified to incorporate long-term (1959–1996) spatially explicit historical fire size and occurrence data as a major model input governing accumulated soil and vegetation carbon stocks. Model outputs of relative magnitudes, seasonal patterns and interannual variability in ET and NPP were verified from eddy covariance tower flux and stand inventory measurements within the study area. For this investigation, simulated annual net primary production (NPP) and evapotranspiration (ET) were used as surrogate variables for forest carbon and water processes, respectively.

2. Materials and methods

2.1. Spatial data collection and study area description

The study area for this investigation encompasses most of the BOREAS region of central Saskatchewan and Manitoba Canada (Fig. 1a). Detailed descriptions of the BOREAS project and study region are provided elsewhere (e.g., Sellers et al., 1997; Hall, 1999), while a summary of spatial data, study area and land cover characteristics relevant to this investigation is provided below. The BOREAS modeling study area covered a regional area of 357,500 km² (52°N to 57°N and 96°W to 107°W) with a rectangular model simulation grid of 66 columns and 60 rows and 10 ft × 5 ft (~10 km²) pixel size. Spatially gridded digital data sets required for model inputs were assembled and re-projected over the study grid; these data included digital elevations, daily surface meteorology from 1994 to 1996, and land cover class information for the study region. All of these data had previously been assembled and published for BOREAS follow-on investigation activities (Newcomer et al., 2000; Genovese and Pauwels, 2001; Nickerson et al., 2002). The land cover maps were derived from a 1 km resolution, 1992 multi-temporal NOAA AVHRR NDVI-based land cover classification (Steyaert et al., 1997). These data were resampled to a 10 ft × 5 ft pixel size in which each pixel represented the dominant land cover class within a 10 ft × 5 ft window (Fig. 1a). The 1 km land cover classification highly generalizes the boreal environment, with specific bias in the extent of wetlands and in distinguishing between wet and dry conifer forest types as compared to a 30 m classification of the same region (Steyaert et al., 1997). Similarly, resampling the 1 km resolution land cover to a 10 ft × 5 ft pixel size further simplifies a complex boreal land cover mosaic. Previous land cover scaling studies of the same region and time period using
BIOME-BGC indicate that errors in model simulations of monthly fluxes can range up to 48% for NPP as the spatial scale of input land cover information is progressively coarsened from 30 m to 50 km scales; however, land cover scale effects on annual NPP and ET fluxes are relatively small (i.e., <15%) because coarse scale overestimation errors during spring are partially offset by underestimation of fine scale results during summer and winter (Kimball and Running, 1999).

Daily meteorological data were assembled from surface weather station network measurements and numerical weather forecast model predictions for the region, and included surface air temperature, precipitation, solar radiation and atmospheric humidity. The mesoscale regional surface meteorological data generally showed lower maximum (mean difference: −0.6 °C) but higher minimum (+2.0 °C) and average (+0.72 °C) daily air temperatures and less solar radiation (−77 W m⁻²) than corresponding site measurements of surface meteorology for the three flux tower sites within the study area (Table 1).

The study region is composed of several major boreal land cover types including wet conifer, dry conifer, deciduous broadleaf forest, mixed deciduous and coniferous forest, and grassland/agricultural vegetation (Steyaert et al., 1997). Wet conifer forest vegetation is predominantly composed of black spruce (Picea mariana) located in low-lying areas with poorly drained soils covered by mosses (Sphagnum spp.) and interspersed with bogs, fens and tamarack (Larix laricina). Dry conifer forests are largely composed of jack pine (Pinus banksiana Lamb.) underlain by lichens (Cladina spp.) and located

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Table 1
Annual means and error statistics of observed local and gridded regional daily meteorology at the NOBS, SOAS, and SOBS flux tower sites for 1994–1996

<table>
<thead>
<tr>
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<td>Error (%)</td>
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<td>−48</td>
<td>55</td>
<td>4</td>
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<td>−21</td>
<td>−37</td>
<td>−3</td>
<td>−19</td>
<td>−21</td>
<td>0</td>
<td>−21</td>
</tr>
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<td>−9.6</td>
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<td>−3.6</td>
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<tr>
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<td>−8.4</td>
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<td>225</td>
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<td>Error (%)</td>
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<td>−21</td>
<td>−39</td>
<td>−39</td>
<td>−19</td>
<td>−39</td>
<td>−39</td>
<td>−19</td>
</tr>
</tbody>
</table>

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(a) Value observed at the flux tower sites.
(b) Value used for input meteorology for regional-scale BIOME-BGC simulations (Nickeson et al., 2002).
(c) Percent of relative error ((Model − Tower)/Tower).
on well-drained sandy soils in upland areas. Deciduous broadleaf forest is dominated by aspen (Populus tremuloides) interspersed with birch (Betula papyrifera), balsam poplar (Populus balsamifera), black spruce, jack pine and white spruce (Picea glauca) stands over generally well drained glacial deposits. The grassland/agricultural land cover class is predominantly located in the southern portion of the study region and is composed of rangeland, pasture, grain and hay production areas, as well as isolated stands of aspen. The study region is relatively flat with gently rolling topography and elevations decreasing in a general southwest to northeast direction.

Climate characteristics, as derived from the 3-year gridded meteorological database, followed a general latitudinal gradient with mean annual maximum and minimum daily air temperatures decreasing from 7.8 °C to 2.0 °C and from −1.8 °C to −7.7 °C from southern to northern portions of the study region, respectively. Mean daytime short-wave solar radiation was higher in the south (445 W m⁻²) relative to the north (417 W m⁻²), while annual precipitation ranged from 412 to 726 mm year⁻¹ across the region without a distinct spatial trend.

### 2.2. Historical fire activity

Historical fire data were obtained from a spatially explicit digital fire history of boreal Canada and North America (Stocks et al., 2002; McGuire et al., 2004). These data contain spatially and temporally explicit fire information, including geographic coordinates of the central locations of burned areas, dates of fire initiation, burning duration, and aerial extents of fires on an annual basis from 1959 to 1997. These data were re-projected onto the study region spatial grid and used to extract annual fire occurrence and burned area information for each fire on a pixel-by-pixel basis across the study region (Fig. 1b). The burned area for each fire was assumed to be circular in shape, with central location and radius defined by fire history location and burned area information (Stocks et al., 2002). For each fire, a given pixel was classified as burned if at least 50% of the pixel was encompassed by a given fire. However, any pixel in which a given fire originated was classified as burned regardless of fire size. Consequently, the cumulative (1959–1996) mapped burned area overestimated actual cumulative burned area by approximately 22%. For each year during the 1959 to 1996 study period, all pixels were classified as either burned (flag 1) or unburned (flag 0) using the historical fire information to produce spatially explicit binary maps of annual burned areas.

Analyses of these data indicate that fire activity shows a considerable degree of spatial and interannual variability within the study region (Figs. 1b and 2a). Over the last 40 years, approximately 50% of the study area experienced fire at least once, while 22% of the region has been burned more than twice. These results are generally consistent with other regional assessments including satellite remote sensing of fire activity for the Canadian boreal forest (Cihlar et al., 1997; Amiro et al., 2001). The annual area burned has also increased more rapidly than annual fire occurrence, indicating that the average size of individual fires has increased over the last 40 years (Fig. 2a). These results also indicate that a total of 7280 km² (2% of total study area) have burned annually within the study region from 1959 to 1996. The relative locations of fire activity include 2030 km² (2% of total wet conifer areas) within wet conifer areas, 3882 km² (3%) within dry conifer, 746 km² (2%) within deciduous forest, 404 km² (2%) within mixed forest and 195 km² (0.6%) within grassland areas, respectively, based on a comparison between historical fire locations and current (circa 1992) land cover characteristics (Fig. 2b). These data also indicate that overall, recent fire activity within the study region is occurring with greater frequency and intensity. These patterns are consistent with other observations (e.g., Wotton and Flannigan, 1993) that both fire occurrence and annual area burned has increased over the last 40 years, especially, since the late 1970s.

### 2.3. Model description and modification

BIOME-BGC is a general ecosystem process model designed to simulate fluxes and storage of water, carbon and nitrogen for terrestrial biomes ranging from single plot to global scales. Details of the model are presented elsewhere and include applications for multiple biome types and spatial scales (e.g., Thornton et al., 2002; White et al., 2000). The model is designed to realistically simulate soil–plant carbon (C) and nitrogen (N) cycling, but with simplifying assumptions to facilitate application at regional scales using a limited number (34) of biome specific physiological constants. All plant, litter, and soil carbon, nitrogen, and water pools and fluxes are entirely prognostic. The plant/ecosystem surface is represented by single, homogenous canopy, snow (when present) and soil layers, where understory vegetation is not distinguished from the aggregate canopy layer. The model also uses a daily time-step with daily maximum and minimum air temperature and precipitation as the primary inputs from which mean daily short-wave radiation, vapor pressure deficit, and day/night average temperatures are estimated. Biophysical processes represented by the model include: photosynthetic C fixation from atmospheric CO₂; N uptake from the atmosphere and soil; C/N allocation to growing plant parts; seasonal phenology, decomposition of fresh plant litter and soil organic matter; plant mortality, growth, litterfall, decomposition and disturbance (i.e., fire and management); solar radiation interception and partitioning into sunlit and shaded leaf fractions; rainfall routing to leaves and soil; snow accumulation and melting; drainage and runoff of soil water; evaporation of water from soil and wet leaves; ET partitioning into transpiration, snow, soil and canopy evaporation components. The BIOME-BGC model has been successfully applied and validated over a range of diverse biomes, spatial scales and climate regimes (e.g., White et al., 2000), including individual boreal forest stands and sub-regions within the BOREAS study region (Kimball et al., 1997a,b, 1999, 2000; Amthor et al., 2001; Potter et al., 2001).

In BIOME-BGC (Thornton, 1998), annual fire mortality rate is specified as a biome specific physiological parameter and remains constant during the simulation. In this study, we modified the model to incorporate spatially and temporally explicit historical fire data as a major input for computing annual fire mortality. This new feature is designed to read binary (1, 0)
annual fire occurrence maps described above and to set daily fire mortality and fire occurrence as a prescribed fraction of carbon burned. We did not explicitly account for dates, duration, and severity of fire. Instead, we assumed: (1) a constant fraction of biomass burned by each individual fire; (2) this fraction of biomass is consumed over a whole year at a constant daily rate of fire consumption; (3) no fire consumption occurs without fire; (4) fire consumes leaf and stem biomass, forest floor litter, and coarse woody debris with an aboveground fire consumption rate, while a smaller belowground fire consumption rate was applied for fine and coarse root biomass. In this study, the carbon fraction consumed by fire was set to a constant fraction (0.26 and 0.06 year$^{-1}$ for aboveground and belowground biomass, respectively) for Canadian boreal forests following McGuire et al. (2004).

2.4. Simulation experiments

We designed a series of simulation sensitivity experiments, summarized in Table 2, to examine the individual and combined effects of historical fires, increasing atmospheric CO$_2$ concentrations and climate change on relative magnitudes and spatial and temporal patterns of boreal net primary production (NPP) and evapotranspiration (ET). Historical atmospheric CO$_2$ concentrations were defined from statistical analysis of Mauna Loa flask measurements and ice core data (Enting et al., 1994; Wigley, 2000) and ranged from 286.9 ppm (1862) to 361.7 ppm (1996). The historical annual fire maps from 1959 to 1996 were prepared as described above. A gridded daily surface meteorological database from 1994 to 1996 (Genovese and Pauwels, 2001; Nickeson et al., 2002) was used to initialize model simulations and define model historical daily meteorological inputs from 1862 to 1996. To extend fire and meteorological inputs over the entire 135-year simulation period, we prescribed a constant fire mortality rate (defined as spin-up simulations) prior to 1959 and then incorporated dynamic rates defined from historical fire disturbance inputs from 1959 to 1996, while the 3-year gridded daily meteorological data set was continuously cycled through the entire (1862–1996) simulation period.
Model simulations of boreal NPP and ET sensitivity to climate variability were investigated using 9 different climate scenarios: historical climate (1994–1996, Control); 2 °C increase (T+) and decrease (T−) in daily air temperature; 20% increase (P+) and decrease (P−) in daily precipitation; 2 °C increase in temperature and 20% increase in precipitation (T+P+); 2 °C decrease in temperature and 20% decrease in precipitation (T−P−); 2 °C increase in temperature and 20% decrease in precipitation (T+P−); 2 °C decrease in temperature and 20% increase in precipitation (T−P+). The relative magnitudes of these temperature and precipitation changes were determined from an evaluation of the 3-year interannual climate variability for three eddy covariance flux tower sites (i.e., Table 1) located within the study region. These changes are consistent with previous BOREAS ecosystem model intercomparison and sensitivity studies (e.g., Potter et al., 2001) and the ranges of long-term (50–100 years) predictions of climate variability for the region (Kattenberg et al., 1996; Kirschbaum and Fischlin, 1996).

The following additional model simulation experiments were conducted to evaluate boreal NPP and ET sensitivity to the individual and combined effects of historical patterns of fire and increasing atmospheric CO₂, and climate variability (see Table 2): NPP/ET simulated under constant atmospheric CO₂ (286.9 ppm) conditions without historical fires and altered climate (NPP/ET-background); NPP/ET simulated under observed increasing atmospheric CO₂ concentrations without historical fires and altered climate (NPP/ET-CO₂); NPP/ET simulated under observed increasing atmospheric CO₂ concentrations and historical fires but without altered climate (NPP/ET-fire); NPP/ET simulated with increasing atmospheric CO₂ concentrations and altered climate but without historical fires (e.g., NPP/ET-(T+P−)).

We isolated the relative impacts of each scenario by conducting the following comparisons: (1) the effect of increasing atmospheric CO₂ by comparing NPP/ET-CO₂ with NPP/ET-background; (2) the sensitivity to altered climate by comparing NPP/ET simulated under adjusted climate conditions (e.g., NPP/ET-(T+P−)) with NPP/ET-CO₂, and (3) the effect of historical fires by comparing NPP/ET-fire with NPP/ET-CO₂. Consequently, a total of 36 distinct simulation scenarios were conducted to isolate the relative effects of these impacts on NPP and ET simulations for the study region. Among 135-year simulations, evaluations of NPP and ET sensitivity to historical CO₂ effects and climate variability were based on mean annual model results from 1994 to 1996, while sensitivity to historical fires was evaluated using mean annual model results from 1959 to 1996.

### Table 2

<table>
<thead>
<tr>
<th>Experiment</th>
<th>CO₂</th>
<th>Fire</th>
<th>Temperature (T)</th>
<th>Precipitation (P)</th>
<th>Description</th>
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<tbody>
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<td>Constant</td>
<td>Constant</td>
<td>Control</td>
<td>Control</td>
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<td>Constant</td>
<td>Control</td>
<td>Control</td>
<td>Increasing CO₂</td>
</tr>
<tr>
<td>NPP-fire</td>
<td>Increasing</td>
<td>Historical</td>
<td>Control</td>
<td>Control</td>
<td>Increasing CO₂, historical fire</td>
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<td>Constant</td>
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<td>Control</td>
<td>Increasing CO₂, increased T</td>
</tr>
<tr>
<td>NPP-(P+)</td>
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<td>Constant</td>
<td>−2 °C</td>
<td>Control</td>
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<tr>
<td>NPP-(P−)</td>
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<td>Constant</td>
<td>Control</td>
<td>−20%</td>
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<td>NPP-(T+P+)</td>
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<td>+20%</td>
<td>Increasing CO₂, increased T and P</td>
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<td>NPP-(T−P−)</td>
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<td>Constant</td>
<td>−2 °C</td>
<td>−20%</td>
<td>Increasing CO₂, decreased T and P</td>
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<td>−20%</td>
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</tbody>
</table>

The ‘CO₂’, ‘Constant’ and ‘Increasing’ column labels specify the use of fixed CO₂ (286.9 ppm) and the historical record of increasing atmospheric CO₂ concentration from 286.9 to 361.7 ppm, respectively; the ‘Fire’, ‘Constant’ and ‘Historical’ column labels indicate the use of constant fire mortality and historical fire data, respectively; the ‘Temperature’, ‘Precipitation’ and ‘Control’ columns indicate the use of historical (1994–1996) meteorology, while ±2 °C and 20% labels indicate the use and level of adjusted air temperature and precipitation meteorology.

### 2.5. Model initialization and validation

BIOME-BGC simulations were conducted by first running the model to steady-state ecosystem carbon and nitrogen pool conditions under continuous 3-year (1994–1996) gridded daily meteorological data cycles and fixed pre-industrial atmospheric CO₂ concentration levels (286.9 ppm). The results of these model spin-up runs were then used as the initial conditions for additional simulations that were conducted from 1862 to 1996 to examine boreal ecosystem responses to different combinations of historical patterns of increasing atmospheric CO₂ concentrations (1862–1996), historical fire disturbance (1959–1996), and climate change scenarios summarized in Table 2. Annual fire mortality for the model spin-up runs and model simulations from 1862 to 1958 was set to a constant rate of 0.01 year⁻¹ for dry conifer and grassland land cover classes and 0.005 year⁻¹ for wet conifer and deciduous forest classes, respectively (Amiro et al., 2001). All other ecophysiological parameters were derived from previous studies conducted within the BOREAS region (e.g., Kimball et al., 1997a,b, 1999). We assumed that the mixed-forest land cover class was composed of 50% deciduous, 25% dry conifer, and 25% wet conifer trees, respectively (Steyaert et al., 1997). For mixed forest pixels, the model was run separately for each of these three different forest types and the results were averaged based on the relative proportion of each land cover class represented.

Model simulations of 1994–1996 daily evapotranspiration fluxes under historical atmospheric CO₂ conditions (ET-CO₂) were compared with corresponding BOREAS tower eddy
covariance measurements of ET at northern old black spruce (NOBS), southern old aspen (SOAS) and southern old black spruce (SOBS) Ameriflux tower sites located within the study region. Detailed information regarding these sites and associated flux and biophysical measurements is provided by Hogg et al. (1997), Jarvis et al. (1997), and Gower et al. (1997). Model NPP simulations were compared with 1993–1994 biomass inventory based estimates of aboveground NPP (ANPP) and total NPP for selected sites within the study region as reported by Gower et al. (1997). These values were compared with simulated mean (1994–1996) annual NPP at these site locations for additional model verification of regional patterns and relative magnitudes of annual fluxes among major land cover classes within the study region.

3. Results

3.1. Comparison of model predictions with flux tower and stand inventory measurements

Model outputs (ET-CO2) were compared with tower eddy covariance based ET (mm day\(^{-1}\)) for three mature forest flux tower sites (NOBS, SOAS, and SOBS) (Table 3). Overall, model predictions were generally coincident with relative magnitudes, and seasonal and interannual patterns of tower based observations at the three sites (Fig. 3). The model results accounted for approximately 61% \((p<0.05)\) of 5-day mean variations of ET observed at the three sites for 1994–1996, respectively; 73% for NOBS; 74% for SOAS; 68% for SOBS. For 1994–1996, mean daily biases in ET results ranged from \(-0.4\) to \(0.3\) mm day\(^{-1}\), while daily mean absolute errors were between \(0.4\) and \(0.8\) mm day\(^{-1}\) (Table 3). Model simulations of seasonal ET variability for the northern and southern old black spruce sites (NOBS and SOBS) generally underestimated tower based results, with larger departures occurring during the summer months. A basis for this discrepancy is that BIOME-BGC does not simultaneously account for the dynamics of both vascular and non-vascular strata that widely coexist at the black spruce sites. Hence, model simulations for the black spruce sites do not include effects of non-vascular strata (i.e., mosses and lichens) on ET. Much of the observed differences between model and tower based estimates of these fluxes were also due to differences in daily meteorological conditions between site observations and the relatively coarse gridded meteorological data set used to drive model simulations (Table 1). Previous model simulations for these sites were generally more consistent with tower flux observations when driven with site meteorological data (e.g., Kimball et al., 1997a,b; Amthor et al., 2001). Despite considerable differences between observed and regional meteorological data, model predictions derived from both meteorological data sources showed equivalent accuracies relative to observed ET for NOBS, SOAS, and SOBS sites, respectively (Table 3).

Overall, model predicted annual NPP results under historical CO\(_2\) conditions (NPP-CO2) were approximately 10% greater than BOREAS stand inventory based NPP estimates for sites

<table>
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<th>Statistics</th>
<th>NOBS</th>
<th>SOAS</th>
<th>SOBS</th>
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<tr>
<td>MAE(^a)</td>
<td>0.8 ((0.5))</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Bias (^d)</td>
<td>(0.5)</td>
<td>(0.3)</td>
<td>(0.5)</td>
</tr>
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<td>((0.02))</td>
<td>(−0.01)</td>
<td>(0.04)</td>
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Model predictions were conducted using regional and tower-observed meteorology, respectively.

\(^a\sum\) (Model−Tower)/No. measurements.

\(^b\) ET predicted using regional meteorology.

\(^c\) ET predicted using observed tower meteorology.

\(^d\) \(\sum\) (Model−Tower)/No. measurements.

Fig. 3. Comparison of 1994–1996 tower eddy covariance and BIOME-BGC estimated ET (mm day\(^{-1}\)) derived using the historical record of increasing atmospheric CO\(_2\) for the (a) NOBS, (b) SOAS, and (c) SOBS flux tower sites. A 5-day moving average of daily results is presented for graphic enhancement. The dot symbols represent eddy covariance based 5-day mean ET from the NOBS, SOAS, and SOBS sites, while solid lines represent 5-day moving averages of BIOME-BGC predicted ET.

Table 3

<table>
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<tr>
<th>Mean absolute error (MAE) and biases between observed and predicted evapotranspiration (ET, mm year(^{-1})) at the NOBS, SOAS, and SOBS flux tower sites for 1994–1996</th>
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<tr>
<td>MAE(^a)</td>
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representative of major vegetation classes within the region (Fig. 4). Whereas, the simulation results under historical CO2 and fire conditions (NPP-fire) were approximately 6% higher and 3% smaller than inventory measurements and simulation results under historical CO2 conditions, respectively. NPP-CO2 for aspen and jack pine stands were approximately 32% and 31% greater than inventory based NPP estimates, respectively, while model results were 34% smaller than inventory based results for black spruce vegetation. Whereas, NPP-fire was 28% (aspen) and 24% (jack pine) greater and 35% (black spruce) smaller than inventory based NPP estimates. These differences are partly due to differences in the respective methods of interpreting aboveground NPP and biomass to carbon conversion ratios, as well as the extreme spatial heterogeneity in inventory-based measurements (Gower et al., 1997) and the relatively coarse spatial scale of the model simulations. Nevertheless both inventory methods and model results show similar differences in relative magnitudes of NPP among the major land cover classes represented.

3.2. Effects of increasing CO2

Both NPP-CO2 (Fig. 5a) and ET-CO2 (Fig. 5b) showed considerable spatial variation within the study area. While
land cover type was a primary control on simulated NPP and ET spatial distributions, regional climate gradients of air temperature and solar radiation also accounted for additional spatial variability in simulated fluxes within each land cover class. For example, dry conifer forests showed distinct gradients of decreasing annual NPP and ET from the southern to northern portions of the study region (Figs. 1 and 5).

Mean annual (1994–1996) NPP-CO2 ranged from 74 to 729 g C m$^{-2}$ year$^{-1}$ and was highest for deciduous forest (505 ± 146 g C m$^{-2}$ year$^{-1}$) vegetation and showed a regional mean of approximately 295 (±123) g C m$^{-2}$ year$^{-1}$ (Fig. 5a and c; Table 4). Results for ET-CO2 ranged from 135 to 466 mm year$^{-1}$ with a regional mean of 298 (±84) mm year$^{-1}$ (Fig. 5b and d; Table 4). Wet conifer vegetation showed a lower annual ET rate (180 ± 15 mm year$^{-1}$) than the other vegetation classes, which ranged from 301 to 372 mm year$^{-1}$ over the 3-year study period (Table 4). Resulting ratios of annual NPP to ET (i.e., a surrogate for water use efficiency defined as the ratio of photosynthesis to water loss in transpiration) for the various land cover classes were highest for deciduous forest (1.68 g C m$^{-2}$ mm$^{-1}$), compared to wet conifer (0.87), dry conifer (0.86), and grassland (0.84) vegetation classes.

Overall, historical increases in atmospheric CO2 enhanced both NPP (mean increase: +33.0 g C m$^{-2}$ year$^{-1}$) and ET (+15.2 mm year$^{-1}$) by approximately 13% and 5% over background conditions, respectively. Deciduous forest showed the largest NPP response (73.8 g C m$^{-2}$ year$^{-1}$, 17%) to increasing atmospheric CO2, followed by dry conifer (35.2 g C m$^{-2}$ year$^{-1}$, 13%), wet conifer (19.8 g C m$^{-2}$ year$^{-1}$, 14%) and grassland (3.8 g C m$^{-2}$ year$^{-1}$, 1%) vegetation classes, respectively (Table 4). In contrast, positive ET responses to increasing
atmospheric CO₂ were highest for dry conifer (23.4 mm year⁻¹, 7%) and lowest for grassland (0.6 mm year⁻¹, 0.2%) classes (Table 4). Historical increases in atmospheric CO₂ also enhanced simulated water use efficiencies, as indicated by ratios of annual NPP to ET, by approximately 8% (+0.07 g C m⁻² mm⁻¹) over background conditions for the entire study region and by approximately 9% (+0.14) for deciduous forest, 10% (+0.08) for dry conifer forest, 5% (+0.04) for wet conifer forest, and 1% (+0.01) for grassland vegetation classes. These increased water use efficiencies for the region were primarily due to the relatively large, positive CO₂ fertilization effect on photosynthesis and NPP compared to positive ET responses to related increases in LAI. Historical increases in atmospheric CO₂ enhanced LAI by approximately 9% (+0.3 m m⁻²) over background conditions for the entire study region: 6% (+0.2) for deciduous forest, 12% (+0.5) for dry conifer forest, 15% (+0.5) for wet conifer forest, and 1% (+0.0) for grassland vegetation classes, respectively. Deciduous forests showed the largest positive NPP response under historical conditions relative to the other vegetation classes, but intermediate increases in LAI and ET, which resulted in the largest increase in water use efficiency.

3.3. Climate sensitivity of boreal NPP and ET

Model simulations of NPP and ET sensitivities to air temperature (T) and precipitation (P) changes varied strongly across the study area depending on land cover type and climatic gradients. Sample sensitivity maps of NPP and ET shown in Fig. 6 show that the largest positive and negative responses of NPP and ET to climate change occurred under T+P+ (both T and P elevated) and T–P– (both T and P decreased) scenarios, respectively; NPP exhibited greater sensitivity to air temperature changes, while ET was more sensitive to changes in precipitation within the ranges of the climate change scenarios (e.g. ±2 °C for T and ±20% for P) applied in this study. The general pattern of ET response to these changes showed marked differences among individual land cover types relative to the response pattern of NPP.

Overall, NPP increased under elevated air temperatures and decreased under cooler air temperature conditions regardless of changes in precipitation (Fig. 7a). Changes in both air temperature and precipitation resulted in greater spatial variability and relative magnitude of NPP response (range: −322% to 17%; standard deviation: 11.1%) than individual changes to either temperature or precipitation (range: −15% to 10%; standard deviation: 8.3%). Deciduous forest and grassland areas showed greater NPP sensitivities to these changes than wet and dry conifer forests. In contrast, the relative response pattern of ET to these changes was distinctly different than NPP (Fig. 7b). The relative ET response was greatest for deciduous conifer forests, while the response of ET to changes in precipitation was greater than the response to air temperature. Interestingly, these sensitivity patterns were similar to the land cover class specific patterns of response to increasing CO₂ (Fig. 5b and c); these results indicate that boreal vegetation, particularly broadleaf deciduous and dry conifer forests, exhibit marked sensitivities and distinct ecophysiological responses to elevated atmospheric CO₂ and air temperature and precipitation changes that appear to be accompanying regional climate change. In addition, the relative effects of increasing air temperatures on NPP are either reinforced or offset by accompanying increases or decreases in precipitation, respectively. For example, our simulations showed that under increased air temperatures, corresponding increases in precipitation enhanced NPP by approximately 9%, while NPP increased by only 1% when warmer air temperatures were accompanied by precipitation reductions. Likewise, regional ET simulations responded accordingly, showing relative changes of approximately +15% and −6% under +T+P and +T–P scenarios, respectively.

3.4. Effects of biomass burning from 1959 to 1996

A subset of the boreal fire disturbance simulations spanning a series of fires in 1961, 1962, 1967, and 1980 illustrates the relative impact of fire on vegetation LAI, NPP, and soil N mineralization rates for the major land cover classes (Fig. 8). Fire resulted in considerable reductions in annual maximum LAI (LAI_max), which was accompanied by concurrent decreases in NPP (e.g., Fig. 8, column 1) and ET (Fig. 9). These results indicate that post-fire LAI_max recovery rates for deciduous forest and grassland vegetation types were relatively

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**Fig. 7.** Land cover class specific mean (1994–1996) sensitivity of (a) NPP and (b) ET to prescribed climate scenarios of altered precipitation (P, ±20%) and air temperature (T, ±2 °C) where: (P+) represents increased P; (T+) represents increased T; (T+P+) represents increased P and T; (T+P−) represents decreased P but increased T; (P−) represents decreased P; (T−) represents decreased T; (T−P+) represents increased P but decreased T; and (T−P−) represents decreased P and T (refer to Table 2 for a summary of abbreviations). Values for the y-axis represent the percent change of NPP/ET simulated using prescribed climate scenarios from NPP/ET-CO₂ simulation results. Vertical bars represent standard deviations of model results.
rapid compared to wet and dry conifer forest classes. During the disturbance-recovery period, forest vegetation classes showed high correlations between LAImax and NPP (\(r^2 = 0.85\) for WC; 0.89 for DC; 0.96 for DEC, \(p < 0.01\)), indicating that NPP reductions following fire are primarily due to decreases in photosynthetic biomass. In contrast, vegetation productivity per unit of photosynthetic biomass (NPP LAImax\(^{-1}\)) and soil N mineralization rate (N_min, kg N m\(^{-2}\) year\(^{-1}\)) both increased following fire disturbance as indicated in Fig. 8 (column 2), but with variable responses depending on vegetation type.

Fire disturbance generally increased the input of organic N to the soil, increasing soil N mineralization (N_min) and availability for plant uptake. Our simulations also showed that for every vegetation type, N_min increased immediately following fire occurrence. Similarly, fire disturbance enhanced vegetation productivity per unit photosynthetic biomass (NPP LAImax\(^{-1}\)), but the response rates varied among different vegetation types, from an immediate productivity response for deciduous forest and grasslands to more than a 10-year time lag for wet and dry conifer forests. Consequently, N_min accounted for most of the annual variability in NPP LAImax\(^{-1}\) for deciduous forest and grassland vegetation types (\(r^2 = 0.87\) and 0.86, \(p < 0.01\), respectively), while N_min showed relatively low correspondence (\(r^2 \leq 0.01\)) to NPP LAImax\(^{-1}\) for wet and dry conifer forests.

Deciduous forests and grasslands exhibited a more rapid productivity response to increased soil N availability following fire disturbance because of shorter leaf canopy turnover rates of deciduous vegetation relative to evergreen coniferous forest classes. Model simulations of leaf N content and associated productivity response to fire coincided closely with the time...
required for complete canopy turnover, which varied from 1 to 10 years for deciduous and evergreen vegetation classes, respectively. We used the 10-year mean $N_{\text{min}}$ rate ($N_{\text{min}}_{10}$) as a surrogate for leaf N accumulation to examine the effect of post-fire soil N mineralization on NPP $\text{LAI}_{\text{max}}^{-1}$ for coniferous evergreen forest classes as shown in Fig. 8 (dotted lines in column 2). Overall, $N_{\text{min}}_{10}$ explained 41% and 25% ($p<0.05$) of annual variations in NPP $\text{LAI}_{\text{max}}^{-1}$ for wet and dry conifer forest classes, respectively. During decreasing and increasing phases of $\text{LAI}_{\text{max}}$, $N_{\text{min}}_{10}$ showed distinctly different relations with NPP $\text{LAI}_{\text{max}}^{-1}$ and explained over 65% ($p<0.05$) of annual variations in NPP $\text{LAI}_{\text{max}}^{-1}$ (e.g., Fig. 8, column 3).

As with NPP, ET decreased immediately following fire disturbance and then recovered as LAI increased. ET recovery rates also varied among different vegetation classes, exhibiting relatively slow recovery rates for wet and dry coniferous forests, and rapid recovery rates for deciduous forest and grassland vegetation (Fig. 9). The ET reduction by the series of fire disturbances was the greatest for dry conifer forest (38%), followed by wet conifer forest (18%), deciduous forest (9%), and grassland (2%) vegetation types. Negative post fire ET responses were largely due to transpiration, which represented a majority (29–67%) of annual ET and showed a direct correspondence to LAI. For each vegetation class, however, soil evaporation generally increased following fire disturbance.

Model simulation results showed an average annual (1959–1996) biomass loss to the atmosphere from historical fire activity of 596 kt C year$^{-1}$ for the entire study region. This amount of biomass loss was equivalent to approximately 6% of mean annual (1959–1996) NPP (Fig. 10). Areas currently occupied by dry conifer forests appeared to be the most susceptible to frequent fire activity, with annual fire consumption of 331 kt C year$^{-1}$, which was equivalent to 8% of the estimated annual NPP for this land cover class. Areas occupied by deciduous forest, wet conifer forest, and grassland vegetation types showed mean annual biomass losses to fire of approximately 115 (5%), 96 (6%), and 3 (0.2%) kt C year$^{-1}$, respectively (Fig. 10).

In contrast, deciduous forest areas showed the highest amount of annual biomass burned per unit area of approximately 28 g C m$^{-2}$ year$^{-1}$, followed by dry conifer (23), wet conifer (10), and grassland (0.7) vegetation classes, respectively (Fig. 10). The estimated mean annual carbon loss to the atmosphere from fire activity was 17 g C m$^{-2}$ year$^{-1}$ over the entire study region. This value is within the range of annual boreal fire losses suggested by Csiszar et al. (2004) and is also close to average fire losses (20 g C m$^{-2}$ year$^{-1}$) estimated for the North American boreal zone during a large fire year (1980). Model simulations of relatively large average annual carbon releases (g C m$^{-2}$ year$^{-1}$) from fire are partially due to our treatment of relatively small fires (<10 km$^2$), which were included in our historical fire simulations, regardless of whether they were significantly smaller in area than the 10 km$^2$ spatial resolution.
used for this study. In addition, our modeling assumption of constant fire intensity regardless of fire occurrence likely resulted in larger simulated carbon releases than observed conditions because fire intensity is likely to decrease with more frequent fire occurrence.

The relative effect of historical fire was less distinct for NPP than ET because fire related reductions in photosynthesis were partially compensated for by similar reductions in autotrophic respiration. ET differences between ET-fire and ET-CO$_2$ simulations were more closely related to fire frequency for the 1959–1996 period than NPP differences between NPP-fire and NPP-CO$_2$ simulations (Fig. 11). Similarly, a stronger linear relationship was found between fire occurrence and ET difference results (e.g., $r^2=0.99$, $p<0.05$) than NPP difference results ($r^2=0.68$, $p<0.05$) for dry conifer forest vegetation. Non-linear response patterns of NPP to historical fire activity were particularly evident for dry conifer (DC) and deciduous (DEC) forest land cover classes (Fig. 11a).

Overall, historical fire activity produced slightly lower NPP and ET rates, indicated by NPP-fire ($287\pm123$ g C m$^{-2}$ year$^{-1}$) and ET-fire ($291\pm82$ mm year$^{-1}$) simulations, than increasing atmospheric CO$_2$ effects indicated by NPP-CO$_2$ ($295\pm123$) and ET-CO$_2$ ($298\pm84$) scenarios, respectively (Table 4). These results indicate that historical fire activity has released approximately 2% more biomass into the atmosphere than prescribed background fire frequency conditions, while the fertilization effect of historical trends of increasing atmospheric CO$_2$ concentrations have enhanced regional NPP and ET by approximately 13% and 5% over background conditions.

4. Discussion and conclusions

Natural and anthropogenic disturbances are major factors shaping terrestrial ecosystem structure and behavior across multiple spatial scales (Cao and Woodward, 1998; Barber et al., 2000; Bousquet et al., 2000; Serreze et al., 2000). Application of a spatially explicit ecosystem process model across a boreal landscape for this investigation provided ecological perspectives on the relative and combined effects of elevated atmospheric CO$_2$ concentrations, historical fire activity, and related climate (air temperature and precipitation) changes to boreal ecosystem water and carbon exchange processes.

The results of these model simulation experiments indicate that increasing atmospheric CO$_2$ concentrations over the last 100 years have enhanced net primary production (+13%), evapotranspiration (+5%), and water use efficiencies (+8%) within the North American boreal forest (Table 4). Model simulations also showed variable responses to climate change. NPP was found to be more sensitive to air temperature change, while ET was more sensitive to precipitation change within the ranges of introduced adjustments (e.g. $\pm2^\circ$C for $T$ and $\pm20\%$ for $P$) applied in this study. Moreover, potential ecosystem responses to climate change represent the net effect of multiple interacting variables. NPP was enhanced by approximately 9% under the $+T+P$ scenario, while NPP increased by only 1% under the $+T−P$ scenario. Likewise, regional ET simulations showed relative changes of approximately +15% and −6% under $+T+P$ and $+T−P$ scenarios, respectively. Thus the potential effects of increasing air temperature on boreal forest annual NPP and ET are either exacerbated or offset by accompanying precipitation changes (Fig. 7). The results of this study also indicate that deciduous and dry conifer boreal forests are more sensitive to elevated atmospheric CO$_2$ and climate change than wet conifer forest and grassland vegetation types.

Historical fires resulted in reductions in both NPP and ET; however, the relative response of NPP to fire activity was generally smaller due to compensating reductions to both photosynthesis and autotrophic respiration, as well as enhanced productivity rates from temporary increases in plant available N following fire (Fig. 8). Model simulations indicate that historical (1959–1996) fire activity has consumed approximately 6% of annual NPP, while areas currently occupied by dry conifer forests appear to be subject to more frequent boreal fire activity and fire consumption (i.e., approximately 8% of annual NPP) relative to areas currently occupied by other boreal land cover classes. These results imply that dry conifer forest areas are more sensitive to fire disturbance than the other boreal land cover classes, though these findings are limited by our use of a temporally static land cover classification that does not account for temporal land cover changes due to stand replacement and vegetation succession following major fire events. Our results also show that the boreal ecosystem is quite sensitive to these disturbances, overall, and that the
general response of the system to these impacts is spatially heterogeneous depending on disturbance type and pattern, land cover and climate gradients.

Non-linear response patterns of NPP to historical fire activity for dry conifer (DC) and deciduous (DEC) land cover classes (Fig. 11a) indicate that boreal forest productivity is limited by soil N availability (Fig. 8) and hence, productivity is relatively low in areas with low fire frequency where vegetation mortality and N cycling rates are markedly lower than areas with greater fire frequency (Ojima et al., 1994; Peng and Apps, 1999). These results also show that NPP for deciduous forest stands was stimulated by fire, while productivity levels for dry conifer and wet conifer stands were reduced by more frequent fire activity. These different NPP response patterns to fire reflect variable C and N uptake and allocation demands, degrees of fire damage to foliage (i.e., LAI reduction by fire as carried out by the aboveground biomass reduction in BIOME-BGC), and LAI recovery rates among different boreal land cover classes. Model simulations of an enhanced NPP response to fire for deciduous forest vegetation resulted from a temporary increase in soil N, while dry and wet conifer forest productivity decreased because of more severe damage to foliage and relatively slow LAI recovery rates (Fig. 8).

Fire changes the vegetation and structural composition of boreal forests considerably. For example, Zimov et al. (1999) showed shifts in dominance of vegetation growth forms from evergreen plants to herbs, grasses, and deciduous woody species following fire disturbance, which can increase photosynthetic uptake of high latitude forests. In this study, we did not consider the effects of dynamic changes to land cover composition following fire, but only accounted for simple changes in vegetation biomass and structure (e.g., LAI). Currently, very limited information is available regarding regional patterns and duration of dynamic changes in dominance of different species following fire, though future research should consider these impacts to NPP, ET and associated ecosystem processes for complex boreal regions. In addition, fire consumption of soil organic matter (SOM) apart from litter layers was not explicitly considered in this simulation study. The historical fire simulations were also limited by utilizing only two constant fire consumption rates for aboveground and belowground biomass components, respectively, regardless of land cover type and carbon pools (i.e., leaf, stem, litter, woody debris, and fine and coarse root). We also did not evaluate the potential impacts of climate change related adjustments to atmospheric humidity, which can have large impacts on canopy conductance to water vapor and CO₂, and soil water content. Some studies (e.g., Barber et al., 2000) indicate reduced growth of Alaskan white spruce from temperature-induced drought stress, which may be aggravated by drier atmospheric conditions and enhanced vapor pressure deficits. Future regional assessments of boreal responses to climate change will likely improve as dynamic vegetation models and additional interactions among meteorological variables are considered, and the relative accuracy and spatial resolution of regional fire and climatological data sets improve.

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