Carbon and energy exchange by a black spruce-moss ecosystem under changing climate: Testing the mathematical model ecosys with data from the BOREAS experiment

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Abstract. There is some uncertainty whether net ecosystem productivity (NEP) of boreal black spruce forests is positive or negative under current climates and how NEP would change under hypothized changes in future climates. The mathematical model ecosys was used to examine NEP of a boreal black spruce forest by testing rates of C transfer simulated from an integrated set of scientific hypotheses against rates measured with chamber, micrometeorological, isotopic and allometric techniques at the northern old black spruce site of the Boreal Ecosystem-Atmosphere Study (BOREAS). Daily aggregations of modeled and measured hourly C fluxes indicated that NEP rose with solar radiation if air temperatures remained below 15°C, but declined if air temperatures rose above 20°C. Daily NEP was thus largest under the higher radiation and lower temperatures of June, but declined under the lower radiation and higher temperatures of July and August. Yearly aggregations of modeled hourly C fluxes indicated that under current (1994-1996) climate NEP of the 150 year old northern old black spruce site was about 40 (wood) + 15 (soil) = 55 g C m⁻² yr⁻¹. Moss was estimated to contribute about 0.25 of net primary productivity (NPP) at this site and was thus an important component of ecosystem C exchange. The model was then used to predict changes in NEP at the old northern old black spruce site under the IS92a climate change scenario. After 150 years NEP was predicted to be 120 (wood) minus 10 (soil) = 110 g C m⁻² yr⁻¹. Cumulative gains of C under this scenario were predicted to be 5700 (wood) minus 700 (soil) = 5000 g C m⁻² after 150 years. Gains of wood C would be vulnerable to loss by fire and insects, both of which could also increase under warmer climates.

1. Introduction

Boreal coniferous forests may have an important effect on global C balances because of their vast area and large C reserves. Several climate change predictions indicate that warming will be most rapid in the continental regions of the boreal zone and so there is great concern about how the net C storage of these forests will be affected by rising temperatures and atmospheric CO₂ concentrations (C₂). Boreal coniferous forests are currently thought to be sinks for atmospheric CO₂ [Sellers et al., 1997] based on seasonal variation and isotopic analyses of C₂ [e.g. Ciais et al., 1995; Keeling et al., 1995]. However climate effects on C storage are the net result of those on gross primary productivity (GPP) and autotrophic respiration (R₂) of both overstory and understory, and on heterotrophic respiration (R₈) of the forest floor and the soil. The effects of climate on each of these fluxes differ such that the dependence of C storage on climate may be complex and difficult to predict. Goulden et al. [1997] reported that GPP of a black spruce - moss forest in northern Manitoba increased with photosynthetic photon flux density (PPFD) up to 500-700 μmol m⁻² s⁻¹ and with air temperature up to 14°C. A strong stomatal constraint to GPP in this forest type was apparent from midday evaporative fractions (LE/Rn) of only 0.35 to 0.45 measured by Jarvis et al. [1997] and Pattey et al. [1997] in central Saskatchewan. This constraint was also apparent in the low stomatal conductances of black spruce needles (0.025 to 0.035 mol m⁻² s⁻¹) measured by Middleton et al. [1997] and has been associated with low foliar N concentrations rather than low soil water potentials. Goulden et al. [1997] reported that respiration of a black spruce - moss forest increased exponentially with temperature, suggesting that rising temperatures could cause smaller increases in GPP than in R₂ and R₈ that would, beyond a certain point, cause net ecosystem productivity (NEP = GPP - R₂ - R₈) to decline.
The complexity with which C storage depends on climate has led to the use of process-based ecosystem models to examine NEP under current climates and to predict NEP under hypothesized climates. The improvement of these models is a key objective of the Boreal Ecosystem-Atmosphere Study (BOREAS) which is to be achieved by collecting data for mass and energy exchange at temporal and spatial scales appropriate to well constrained model tests [Sellers et al., 1997]. If these tests are successful under current climates, then the confidence with which such models may be used to predict changes in mass and energy exchange under hypothesized climates would be greatly enhanced.

One ecosystem model included in these tests is ecosys [Grant, 1996a, 1996b], output from which has been compared with measurements of diurnal mass and energy exchange and of long term C accumulation in a mixed aspen – hazelnut forest [Grant et al., 1999a] and a spruce – moss forest [Grant et al., 2001] in the southern study area of BOREAS. This model simulates hourly GPP, R_a and R_h as affected by soil and plant temperatures [Grant, 1993a, 1994b; Grant et al., 1993a, 1993b; Grant and Rochette, 1994; Grant et al., 1995b], soil and plant water contents [Grant et al., 1993a, 1993b; Grant and Rochette, 1994], soil and plant N and P concentrations [Grant, 1991, 1998a; Grant and Robertson, 1997], soil and plant aeration [Grant, 1995; Grant et al., 1993c, 1993d; Grant and Pattey, 1999], air temperature and irradiance [Grant, 1992a, 1992b; Grant et al., 1999a].

In this study ecosys was used to study climate effects on NEP in a boreal coniferous forest by comparing hourly model output for C and energy exchange under changing weather conditions with eddy correlation fluxes measured by Goulden et al. [1997] over a 150 year old black spruce – moss forest in northern Manitoba. These ecosystem scale tests were supported by smaller-scale comparisons of C fluxes modeled over the moss surface with fluxes measured in automated chambers by Goulden and Crill [1997], and of CO2 fixation rates modeled at needle surfaces with fixation rates measured in climate - controlled leaf chambers by Berry et al. [1998]. These model tests extend those conducted by Amthor et al. [this issue] as part of an intercomparison of nine ecosystem models. Ecosys was then used to predict NEP of a black spruce – moss forest in northern Manitoba during the next 150 years under an IS92a climate change scenario.

2. Model Development

A detailed description of the algorithms on which ecosys is based, and of the testing to which they have been subjected, is given in Grant, 2001. A general description of those parts of the model most relevant to the study reported here is given below. A summary description of ecosys and other ecosystem models is given in Amthor et al. [this issue].

2.1. Net Primary Productivity

2.1.1. CO2 Fixation. CO2 fixation is calculated in ecosys from coupled algorithms for carboxylation and diffusion. Carboxylation rates are calculated for each leaf surface of multispecific plant canopies, defined by height, azimuth, inclination and exposure (sunlit versus shaded), as the lesser of dark and light reaction rates [Grant et al., 1999b] according to Farquhar et al. [1980]. These rates are driven by irradiance (rectangular hyperbola), temperature (Arrhenius kinetics) and CO2 concentration (Michaelis-Menten function). Maximum dark or light reaction rates used in these functions are determined by specific activities and surficial concentrations of rubisco or chlorophyll respectively. These activities and concentrations are determined by environmental conditions during leaf growth (CO2 fixation, water, N and P uptake) as described in section 2.1.4.

Diffusion rates are calculated for each leaf surface from the CO2 concentration difference between the canopy atmosphere and the mesophyll multiplied by leaf stomatal conductance [Grant et al., 1999b] required to maintain a set C_i: C_a ratio at the leaf carboxylation rate. Stomatal conductance is also an exponential function of canopy turgor generated from a convergence solution for canopy water potential at which the difference between transpiration and root water uptake equals the difference between canopy water contents at the water potentials of the previous and current time steps [Grant et al., 1999b]. Canopy transpiration is solved from a first order solution to the canopy energy balance [Grant et al., 1999b].

2.1.2. Autotrophic Respiration and Senescence. The product of CO2 fixation is added to a pool of stored C for each branch (defined here as a complete subcomponent of a plant including twigs and foliage) of each plant species from which C is oxidized to meet maintenance respiration requirements using a first order function of stored C [Grant et al., 1999b]. If the pool of stored C is depleted, the C oxidation rate may be less than the maintenance respiration requirement, in which case the difference is made up through respiration of remobilizable C in leaves and twigs. Upon exhaustion of the remobilizable C in each leaf and twig, the remaining C is dropped from the branch as litterfall and added to residue at the soil surface where it undergoes decomposition as described in section 2.2. Environmental constraints such as nutrient, heat or water stress which reduce net C fixation and hence C storage will therefore accelerate litterfall. When oxidation of stored C exceeds maintenance respiration, the excess is used for growth respiration to drive the formation of new biomass [Grant et al., 1999b] as described in section 2.1.4.

2.1.3. Nutrient Uptake. Nutrient (N and P) uptake is calculated for each plant species by solving for aqueous concentrations of NH4+, NO3- and H2PO4- at root and mycorrhizal surfaces in each soil layer at which radial transport by mass flow and diffusion from the soil solution to the surfaces equals active uptake by the surfaces [Grant and Robertson, 1997; Grant, 1998b]. This solution dynamically links rates of soil nutrient transformations with those of root and mycorrhizal nutrient uptake. Nutrient transformations control the aqueous concentrations of NH4+, NO3- and H2PO4- in each soil layer through thermodynamically driven precipitation, adsorption and ion pairing reactions [Grant and Heaney, 1997], convective-dispersive solute transport [Grant and Heaney, 1997] and microbial mineralization-immobilization [Grant et al., 1993a]. Active uptake is calculated from length densities and surface areas [Noh and Barber, 1983] given by a root and mycorrhizal growth submodel [Grant, 1993a, 1993b, Grant, 1998b; Grant and Robertson, 1997]. Active nutrient uptake is constrained by O2 uptake [Grant, 1993a,b], by solution NH4+, NO3- and H2PO4- concentrations, and by concentrations of C, N and P stored by root and mycorrhizae [Grant, 1998b]. The products of N and P uptake are stored in root and mycorrhizal pools from which they are combined with stored C when driven by growth respiration to form new plant biomass as described in section 2.1.4. Plant species designated as legumes in the model also grow
root nodules in which aqueous N\textsubscript{2} is reduced to stored N through oxidation of stored C according to the energetics of Schubert [1982]. This reduction generates concentration gradients of stored C, N and P between nodule and root that drives nutrient exchange.

### 2.1.4. Plant Growth

Growth respiration from section 2.1.2 drives expansive growth of vegetative and reproductive organs through mobilization of stored C, N and P in each branch of each plant species according to phenology-dependent partitioning coefficients and biochemically based growth yields. This growth is used to simulate the lengths, areas and volumes of individual internodes, twigs and leaves [Grant, 1994b; Grant and Hesketh, 1992] from which heights and areas of leaf and stem surfaces are calculated for irradiance interception and aerodynamic conductance algorithms used in energy balance calculations. Growth respiration also drives extension of primary and secondary root axes and of mycorrhizal axes of each plant species in each soil layer through mobilization of stored C, N and P in each root zone of each plant species [Grant, 1993a, 1993b, Grant, 1998b]. This growth is used to calculate lengths and areas of root and mycorrhizal axes from which root uptake of water [Grant et al., 1999b] and nutrients [Grant, 1991; Grant and Robertson, 1997] is calculated.

The growth of different branch organs and root axes in the model depends upon transfers of stored C, N and P among branches, roots and mycorrhizae. These transfers are driven by concentration gradients within the plant which develop from different rates of C, N or P acquisition and consumption by its branches, roots and mycorrhizae [Grant, 1998b]. When root N or P uptake rates described in section 2.1.3 are low, stored N or P concentrations in roots and branches become low with respect to those of stored C. Such low ratios in branches reduce the specific activities and surficial concentrations of leaf rubisco and chlorophyll which in turn reduce leaf CO\textsubscript{2} fixation rates. These low ratios also cause smaller root-to-shoot transfers of N and P and larger shoot-to-root transfers of C [Grant, 1998b], thereby allowing more plant resources to be directed towards root growth. The consequent increase in root:shoot ratios and thus in N and P uptake, coupled with the decrease in C fixation rate, redresses to some extent the stored C:N:P imbalance when N or P uptake is limiting. The model thus implements the functional equilibrium between roots and shoots proposed by Thornley [1995].

### 2.2. Heterotrophic Respiration

#### 2.2.1. Decomposition

Soil organic matter in ecosys is resolved into four substrate-microbe complexes (plant residue, animal manure, particulate organic matter and non-particulate organic matter) within each of which C, N and P may move among five organic states: solid substrate, sorbed substrate, soluble hydrolysis products including acetate, microbial communities, and microbial residues [Grant, 1999, Table 1]. Each organic state in each complex is resolved into structural components of differing vulnerability to hydrolysis and into elemental fractions C, N and P within each structural component. Microbial communities are also resolved into functional types including obligate aerobes, facultative anaerobes (dennitrifiers), obligate anaerobes (fermenters), methanogens and diatoms.

Litterfall from section 2.1.2 is added to the plant residue complex and partitioned into carbohydrate, protein, cellulose and lignin structural components according to Trofymow et al. [1995]. Rates of component hydrolysis are the product of the active biomass and specific activity of each microbial functional type within each complex [Grant et al., 1993a; Grant and Rochette, 1994]. Specific activity is constrained by substrate-microbe density relationships [Grant et al., 1993a; Grant and Rochette, 1994], and by the temperatures and water contents of surface residue and a vertically resolved soil profile [Grant, 1997; Grant and Rochette, 1994; Grant et al., 1998]. A fraction of the hydrolysis products of lignin is coupled with those of protein and carbohydrate according to the stoichiometry proposed by Shulten and Schnitzer [1997] and the resulting compound is transferred to the solid substrate of the particulate organic matter complex. Rates of particulate organic matter formation are thus determined by substrate lignin content and heterotrophic microbial activity.

#### 2.2.2. Microbial Growth

The concentration of the soluble hydrolysis products in section 2.2.1 determines rates of C oxidation by each heterotrophic population, the total of which drives CO\textsubscript{2} emission from the soil surface. This oxidation is coupled to the reduction of O\textsubscript{2} by all aerobic populations [Grant et al., 1993a, 1993b; Grant and Rochette, 1994], to the sequential reduction of NO\textsubscript{3}\textsuperscript{-}, NO\textsubscript{2}\textsuperscript{-} and N\textsubscript{2}O by heterotrophic denitrifiers [Grant et al., 1993c,d; Grant and Pattey, 1999] and to the reduction of organic C by fermenters and of acetate by heterotrophic methanogens [Grant, 1998a]. The energetics of these oxidation-reduction reactions determine growth yields and hence the active biomass of each heterotrophic functional type from which its decomposer activity is calculated as described in section 2.2.1. In addition, autotrophic nitrifiers conduct NH\textsubscript{4}\textsuperscript{+} and NO\textsubscript{2}\textsuperscript{-} oxidation [Grant, 1994a] and N\textsubscript{2}O evolution [Grant, 1995], and autotrophic methanotrophs conduct CH\textsubscript{4} oxidation [Grant, 1999], the energetics of which determine autotrophic growth yields and hence biomass and activity. Each microbial population in the model seeks to maintain steady-state ratios of biomass C:N:P by mineralizing or immobilizing NH\textsubscript{4}\textsuperscript{+}, NO\textsubscript{3}\textsuperscript{-}, NO\textsubscript{2}\textsuperscript{-} and H\textsubscript{2}PO\textsubscript{4}\textsuperscript{-}, thereby regulating solution concentrations that drive N and P uptake by roots and mycorrhizae as described in section 2.1.3. Microbial populations undergo first order decomposition, products of which are partitioned between microbial residues within the same substrate-microbe complex, and the solid substrate of the nonparticulate organic matter complex according to soil clay content [Grant et al., 1993a, 1993b]. Rates of nonparticulate organic matter formation are thus determined by rates of microbial decay and by soil clay content.

### 3. Field Experiment

#### 3.1. Site Description

The old black spruce site in the northern study area of BOREAS (55.9°N, 98.4°W) is almost flat, poorly drained, and covered by a dominant canopy of black spruce (Picea mariana (Mill.) BSP), average age 155 years, height 9.1 m, density 5450 ha\textsuperscript{-1} from Gower et al., 1997] with a minor shrub layer and feather moss (Pleurozium schreberi and Hylocomium splendens) in upper locations, and continuous sphagnum moss (Sphagnum spp.) in lower locations. The soils at this site range from Eluviated Eutric Brunisols to Gleyed Cumulic and Cumic Humic Regosols. These soils have a 0.1 - 1.6 m peat layer overlying a coarse-textured mineral soil (Table 1).

#### 3.2. Leaf CO\textsubscript{2} Fixation

On August 5 and 6 1996, selected needle clusters near the top of the black spruce canopy were enclosed in the cuvette of a portable gas exchange system (model MPH-1000, Campbell Scientific, Logan Utah) with an infrared gas analyzer (model...
6262, LiCor Inc., Lincoln Nebraska) and a dew point hygrometer (model Dew-10, General Eastern, Woburn, Massachusetts) that enabled precise control of CO2, temperature, irradiance and humidity at the leaf surface. The leaves were subjected to incremental changes in irradiance or CO2 with all other environmental conditions held constant. Response of CO2 flux to increments of ~50 mol m^-2 s^-1 in irradiance was measured at a CO2 concentration of 360 mol mol^-1, a leaf temperature of 20°C, and a relative humidity of 0.6. Response of CO2 flux to increments of ~100 mol mol^-1 in CO2 concentration was measured at an irradiance of 2350 mol m^-2 s^-1, a leaf temperature of 23.5°C and a relative humidity of 0.5, and again at an irradiance of 650 mol m^-2 s^-1, a leaf temperature of 20.0°C and a relative humidity of 0.3. Measurements of CO2 flux and stomatal conductance were taken once steady-state values were achieved (usually 30 min. after conditions were changed). Further details are reported by Berry et al. [1998].

3.3. Canopy Mass and Energy Exchange

Fluxes of latent heat, sensible heat, CO2 and momentum were measured by eddy correlation at a height of 29 m and a frequency of 4 Hz with a three-axis sonic anemometer and temperature sensor (Applied Technologies, Boulder, Colorado), and an infrared gas analyzer (model 6262, Li-Cor Inc., Lincoln, Nebraska) following Woody et al. [1993] and Goulden et al. [1996]. CO2 and water vapor concentrations measured every 12 min at heights of 0.3, 1.5, 4.6, 8.4, 12.9 and 28.8 m were used to calculate hourly changes in canopy CO2 storage which were added to fluxes measured by eddy correlation to estimate hourly net ecosystem productivity. Soil temperatures were measured with precision thermistors at 0.05, 0.10, 0.20, 0.50 and 1.00 m beneath the moss surface at five sites along a topographic gradient. Details of measurement apparatus, techniques and results are given by Goulden et al. [1997].

3.4. CO2 Exchange Over Moss

An automated gas exchange system sampled air drawn via distribution manifolds through clear 0.38 x 0.385 x 0.25 m chambers inserted to a depth of 0.10 – 0.15 m below the moss surface. Gas samples were taken during 10 min periods after closure of the chambers. Changes in CO2 and water vapor concentrations during this period were measured with an infrared gas analyzer (model 6262, Li-Cor Inc., Lincoln, Nebraska) operating in absolute mode. CO2 fluxes over the moss were estimated by extrapolating changes in CO2 concentrations measured from 2 to 4 min after closure back to the moment of closure. The chambers were then pneumatically raised to a vertical position until the next sampling period 3 hours later. Each chamber was calibrated daily by adding a known CO2 flux to the return flow during sampling. Further details of gas exchange measurements over moss are given by Goulden and Crill [1997].

4. Model Experiment

4.1. Model Initialization and Run

The ecosystem model ecosys was initialized with data for the physical properties of a Cumic Humic Regosol (Table 1), and with values for the biological properties of black spruce and moss (Table 2). These values remained the same as those of aspen and hazelnut used in an earlier study of mass and energy exchange (Grant et al., 1999a, Table 3), except for the following changes:

4.1.1. Spruce. (1) The minimum leaf C:N ratio was raised from 6.67 g g^-1 for broadleaf plants to 20.0 g g^-1 (= 22.5 mg N g DM^-1) for coniferous plants based on foliar N concentrations measured in heavily fertilized black spruce by Mahendrappa and Solonius [1982]. Actual C:N ratios rise above this minimum value if stored C:N ratios limit plant growth in the model. (2) The interception fraction (clumping index) was reduced from 0.65 for aspen to 0.50 for spruce based on irradiance interception data from Chen et al. [1997]. (3) The value of the parameter relating leaf area expansion to leaf mass growth [Grant and Hesketh, 1992, equation (4)] was reduced from that used for deciduous plants based on specific leaf areas measured by Middleton et al. [1997]. (4) Reflection and transmission coefficients for shortwave radiation were reduced from 0.225 for deciduous leaves to 0.15 for coniferous leaves based on data from Betts and Ball [1997]. Reflection and transmission coefficients for photosynthetically active radiation (0.75) were not changed. (5) A model switch used in deciduous trees to force the withdrawal and storage of leaf C, N and P after a cold requirement under shortening photoperiods, and the remobilization of stored nutrients following a heat requirement under lengthening photoperiods was disabled for coniferous trees. (6) Protein, carbohydrate, cellulose and lignin contents of coniferous litter were changed from those of deciduous litter according to Trofymow et al. [1995] (Table 1).

<table>
<thead>
<tr>
<th>Depth (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BD (Mg m^-3)</td>
</tr>
<tr>
<td>0 CO2 (mol m^-3)</td>
</tr>
<tr>
<td>0 H2O (mol m^-3)</td>
</tr>
<tr>
<td>Sand (kg kg^-1)</td>
</tr>
<tr>
<td>Silt (kg kg^-1)</td>
</tr>
<tr>
<td>pH</td>
</tr>
<tr>
<td>CEC (cmol kg^-1)</td>
</tr>
<tr>
<td>Org. C (g kg^-1)</td>
</tr>
<tr>
<td>Org. N (mg kg^-1)</td>
</tr>
<tr>
<td>Org. P (mg kg^-1)</td>
</tr>
<tr>
<td>AI-P (mg kg^-1)</td>
</tr>
<tr>
<td>Ca-P (mg kg^-1)</td>
</tr>
</tbody>
</table>
| abbreviations: BD, bulk density; H2O, water content; CEC, cation exchange capacity; AI-P, aluminium phosphate, calculated from total P – organic P and modeled as variscite; Ca-P, calcium phosphate, calculated from total P – organic P and modeled as hydroxyapatite.
Table 2. Key Biological Properties of Spruce, Moss and Soil Microbial Populations Used in Ecosys

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum carboxylation rate</td>
<td>50</td>
<td>μmol CO₂ g⁻¹ rubisco s⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Maximum rubisco oxygenation rate</td>
<td>10.5</td>
<td>μmol O₂ g⁻¹ rubisco s⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Maximum electron transport rate</td>
<td>500</td>
<td>μmol e⁻ g⁻¹ chlorophyll s⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Quantum efficiency</td>
<td>0.5</td>
<td>μmol e⁻ μmol quanta</td>
</tr>
<tr>
<td>Kₘ for carboxylation</td>
<td>12.5</td>
<td>μM CO₂ at 30 °C</td>
</tr>
<tr>
<td>Kₘ for oxygenation</td>
<td>500</td>
<td>μM O₂</td>
</tr>
<tr>
<td>Transmission &amp; reflection of shortwave radiation</td>
<td>0.15</td>
<td></td>
</tr>
<tr>
<td>Fraction of leaf protein in rubisco</td>
<td>0.075</td>
<td></td>
</tr>
<tr>
<td>Fraction of leaf protein in chlorophyll</td>
<td>0.02 (spruce) 0.67 (moss)</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Minimum C:N ratio in leaf</td>
<td>20.0 (spruce) 6.67 (moss)</td>
<td>g (N) g⁻¹ (C)</td>
</tr>
<tr>
<td>C:N ratio in twig and root</td>
<td>40.0</td>
<td>g (N) g⁻¹ (C)</td>
</tr>
<tr>
<td>C:N ratio in stem</td>
<td>267</td>
<td>g (N) g⁻¹ (C)</td>
</tr>
<tr>
<td>Maximum C:P ratio in leaf</td>
<td>200 (spruce) 60.7 (moss)</td>
<td>g (P) g⁻¹ (C)</td>
</tr>
<tr>
<td>C:P ratio in twig and root</td>
<td>400</td>
<td>g (P) g⁻¹ (C)</td>
</tr>
<tr>
<td>C:P ratio in stem</td>
<td>2667</td>
<td>g (P) g⁻¹ (C)</td>
</tr>
<tr>
<td>Maintenance respiration of plant</td>
<td>0.016</td>
<td>g (C) g⁻¹ (N) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Growth yield of leaf and twig</td>
<td>0.64</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Growth yield of stem</td>
<td>0.76</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Growth yield of root</td>
<td>0.64</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Interception fraction (spruce)</td>
<td>0.6</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>Interception fraction (moss)</td>
<td>1.0</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>C₆C₆ ratio at non-limiting water</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>Maximum root NH₄⁺ uptake rate</td>
<td>0.025</td>
<td>g (N) m⁻² root area h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Kₘ for root NH₄⁺ uptake</td>
<td>0.40</td>
<td>g (N) m⁻²</td>
</tr>
<tr>
<td>Minimum NH₄⁺ conc’n for root uptake</td>
<td>0.03</td>
<td>g (N) m⁻³</td>
</tr>
<tr>
<td>Maximum root PO₄³⁻ uptake rate</td>
<td>0.005</td>
<td>g (P) m⁻² root area h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Kₘ for root PO₄³⁻ uptake</td>
<td>0.075</td>
<td>g (P) m⁻¹</td>
</tr>
<tr>
<td>Minimum PO₄³⁻ conc’n for root uptake</td>
<td>0.002</td>
<td>g (P) m⁻²</td>
</tr>
<tr>
<td>Litterfall protein content</td>
<td>0.07 (spruce) 0.07 (moss)</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Litterfall carbohydrate content</td>
<td>0.27 (spruce) 0.34 (moss)</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Litterfall cellulose content</td>
<td>0.36 (spruce) 0.43 (moss)</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Litterfall lignin content</td>
<td>0.30 (spruce) 0.16 (moss)</td>
<td>g (C) g⁻¹ (C)</td>
</tr>
<tr>
<td>Specific activity of protein decomposition</td>
<td>1.0</td>
<td>g (C) g⁻¹ micr. (C) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Specific activity of carbohydrate decomposition</td>
<td>1.0</td>
<td>g (C) g⁻¹ micr. (C) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Specific activity of cellulose decomposition</td>
<td>0.15</td>
<td>g (C) g⁻¹ micr. (C) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Specific activity of lignin decomposition</td>
<td>0.025</td>
<td>g (C) g⁻¹ micr. (C) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Specific activity of active OM decomposition</td>
<td>0.025</td>
<td>g (C) g⁻¹ micr. (C) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Specific activity of humus decomposition</td>
<td>0.005</td>
<td>g (C) g⁻¹ micr. (C) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Specific respiration rate</td>
<td>0.20</td>
<td>g (C) g⁻¹ micr. (C) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Kₑₑ for microbial C uptake</td>
<td>35</td>
<td>g (C) m⁻¹</td>
</tr>
<tr>
<td>Maintenance resp’n of labile biomass</td>
<td>0.010</td>
<td>g (C) g⁻¹ micr. (N) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Maintenance resp’n of resistant biomass</td>
<td>0.0015</td>
<td>g (C) g⁻¹ micr. (N) h⁻¹ at 30 °C</td>
</tr>
<tr>
<td>Energy yield of C oxid’n with O₂ reduction</td>
<td>37.5</td>
<td>kJ g⁻¹ (C)</td>
</tr>
<tr>
<td>Energy yield of C oxid’n with NO₃ reduction</td>
<td>10.0</td>
<td>kJ g⁻¹ (C)</td>
</tr>
<tr>
<td>Energy yield of C oxid’n with acetate reduction</td>
<td>1.03</td>
<td>kJ g⁻¹ (C)</td>
</tr>
<tr>
<td>Energy requirement for microbial growth</td>
<td>25.0</td>
<td>kJ g⁻¹ (C)</td>
</tr>
<tr>
<td>Requirement of C oxidation for N₂ fixation</td>
<td>6.0</td>
<td>g (C) g⁻¹ (N)</td>
</tr>
</tbody>
</table>

4.1.2. Moss. (1) The shape parameter relating leaf turgor to stomatal resistance used for vascular plants [Grant et al., 1999b, equation (13)] was set to zero for moss, thereby replacing the dynamic stomatal response to turgor with a constant diffusive resistance taken from Proctor [1982]. This constant resistance forced moss water potential to equilibrate with atmospheric relative humidity during the convergence solution for energy exchange. (2) The effect of plant water status on CO₂ fixation in moss was calculated from the relative humidity associated with moss water potential according to data given by Proctor [1982] and in Clymo and Hayward [1982], rather than from stomatal resistance and water potential as in vascular plants.

All other model parameters for C fixation, respiration and partitioning by plant and microbial populations were the same as those used in earlier studies of C and energy exchange over agricultural crops [Grant and Baldocchi, 1992; Grant et al., 1993c, 1995c], forests [Grant et al., 1999a] and soils [Grant, 1994a, 1997; Grant and Rochette, 1994; Grant et al., 1993a,
Table 3. Annual Carbon Balance of a 150 Year Old Black Spruce - Moss Forest in Northern Manitoba Estimated From Flux Measurements and Allometric Techniques During 1994, and Simulated by Ecosys Under 1994, 1995 And 1996 Climate and Under 1996 Climate After 150 Years of IS92a Climate Change

<table>
<thead>
<tr>
<th></th>
<th>Estimated (g C m⁻²)</th>
<th>Simulated (g C m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gross primary productivity</td>
<td>624</td>
<td>600</td>
</tr>
<tr>
<td>Autotrophic respiration*</td>
<td>396</td>
<td>366</td>
</tr>
<tr>
<td>Net primary productivity</td>
<td>228</td>
<td>234</td>
</tr>
<tr>
<td>Senescence 46° + 90°</td>
<td>179</td>
<td>171</td>
</tr>
<tr>
<td>Exudation 20°,78°</td>
<td>26</td>
<td>19</td>
</tr>
<tr>
<td>Net Growth 12°</td>
<td>23</td>
<td>44</td>
</tr>
<tr>
<td>Moss</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gross primary productivity</td>
<td>179</td>
<td>180</td>
</tr>
<tr>
<td>Autotrophic respiration*</td>
<td>108</td>
<td>104</td>
</tr>
<tr>
<td>Net primary productivity</td>
<td>50 – 150°</td>
<td>71</td>
</tr>
<tr>
<td>Senescence 72°</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Exudation 72°</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Net growth 12°</td>
<td>-2</td>
<td>-3</td>
</tr>
<tr>
<td>Change in storage 1</td>
<td>1</td>
<td>-2</td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heterotrophic respiration*</td>
<td>245</td>
<td>243</td>
</tr>
<tr>
<td>Ecosystem</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gross primary productivity</td>
<td>800°,1080°</td>
<td>803</td>
</tr>
<tr>
<td>Total respiration</td>
<td>800°</td>
<td>749</td>
</tr>
<tr>
<td>Net ecosystem productivity</td>
<td>-40°</td>
<td>54</td>
</tr>
<tr>
<td>Net primary productivity</td>
<td>219°,252°</td>
<td>299</td>
</tr>
<tr>
<td>Change in plant C 21°</td>
<td>21</td>
<td>43</td>
</tr>
<tr>
<td>Change in soil C 10 - 30°</td>
<td>33</td>
<td>24</td>
</tr>
</tbody>
</table>

* Includes root respiration
Excludes root respiration
Includes CO₂-C and CH₄-C
Gower et al. (1997) above-ground
Steele et al. (1997) below-ground
Ryan et al. (1997)
Harden et al. (1997)
Goulden et al. (1997)
Alberta Forest Service (1985)
Goulden et al. (1998)

1993b, 1993c, 1995b, 1998]. The values of all model parameters were derived independently of data recorded at the field site.

The lower boundary of the modeled soil profile was set to prevent subsurface drainage or capillary rise. The upper boundary of the modeled soil profile was set to allow fairly rapid surface runoff so that any water accumulating beyond the surface storage capacity of the soil was removed within a few hours. These settings were intended to simulate the hydrology of the field site which had poor subsurface drainage but fairly good surface drainage. The model was then run for 150 years under random yearly sequences of hourly averaged meteorological data (air temperature, humidity and wind speed) recorded at the flux tower during 1994, 1995 and 1996 [Sutton et al., 1998], supplemented with 1 km² gridded data (shortwave radiation and precipitation) generated from surface measurements. Model Cₐ was initialized at 280 µmol mol⁻¹ and incremented daily at a rate of 0.00167 yr⁻¹ so that Cₐ recorded in 1996 would be reached after 150 years. Atmospheric N deposition in the model occurred as NO₃⁻ dissolved in precipitation (0.5 g N m⁻³) and as NH₄⁺ from adsorption of atmospheric NH₃ (0.004 µmol mol⁻¹) by leaves and soil surfaces. During the first year of the run, spruce and moss were seeded onto the forest floor at 0.6 m² [Gower et al., 1997] and 104 m² [Clymo and Hayward, 1982] respectively. No other interventions occurred during the entire run.

4.2. Leaf CO₂ Fixation

After completion of the model run, all state variables in the model were initialized with the values they had held at the end of August 5 in the 150th year of the model run during which 1996 meteorological data had been used. The model was then run for 24 hours under incremental changes in irradiance or Cₐ with all other environmental conditions maintained at values used in the leaf CO₂ fixation study described in section 3. Steady state values for net CO₂ fixation rates (CO₂ fixation - maintenance respiration from Table 2) and stomatal conductances were attained within 12 hourly time steps of the start of each model run. Fixation rates and conductances simulated for an individual leaf surface in the upper part of the spruce canopy were compared with measured values. Because conifer needle surfaces used in the CO₂ fixation study were assumed to be randomly oriented towards incident irradiance, simulated values were taken as the average of those for all leaf orientation classes (azimuth and inclination as described in section 2.1.1) represented in the model.

4.3. Canopy Mass and Energy Exchange

During the same year of the model run as that used in the leaf CO₂ fixation study described above, hourly mass and energy exchange over the spruce-moss stand simulated under 1996 meteorological data were compared with results obtained from
the flux tower at the field site during 1996. Simulated CO₂ and energy fluxes over the spruce were calculated as the sum of those from the soil surface, the surface detritus, the moss and the spruce. Simulated CO₂ and energy fluxes over the moss were calculated as the sum of those from the soil surface, the surface detritus and the moss. Soil temperatures simulated in the midpoint of the detritus layer beneath the moss, and in the organic layer 0.10 m below the midpoint of the detritus layer, were compared with those measured 0.10 and 0.20 m below the surface of the moss. Three one week periods were selected for comparison during 1996. The first was in late spring (June 18-24) to observe model behavior during a transition from clear warm weather to cool cloudy weather. The second was in mid summer (July 25-31) to observe model behavior during a period of clear weather with rising temperatures. The third was in late summer (August 30 to September 5) to observe model behavior when the weather was cooling.

4.4. Long-Term C Exchange

Model results for annual net primary productivity (NPP), net ecosystem productivity (NEP) and aboveground phytomass growth of a 150 year old spruce-moss forest under 1994 climate were then compared with estimates of NPP, NEP and growth derived from aggregated flux data, tree ring analyses and other measurements taken at the field site during 1994. Long-term model results for C accumulation in spruce wood and soil were compared with results from measurements of spruce growth and forest floor development in the same ecological zone as that of the field site.

The model run was then extended for another 150 years using the same soil and plant properties, but with changes in atmospheric boundary conditions selected from Kattenberg et al. [1996]. These changes were applied to the same sequence of hourly-averaged meteorological data used in the first run. A compound increase in Ca of 0.007 yr⁻¹ calculated daily was used to simulate a doubling of concentration over 100 years according to the IPCC IS92a emissions scenario. This increase was accompanied by simple daily increases in maximum and minimum air temperature that depended upon time of day and time of year. Maximum daily temperatures rose more slowly (average 0.0275°C yr⁻¹) than did minimum daily temperatures (average 0.0325°C yr⁻¹) in order to simulate a reduction in temperature ranges caused by increased evapotranspiration and aerosol loading [Kattenberg et al., 1996]. Both maximum and minimum daily temperatures rose more slowly during spring and summer than during autumn and winter [Kattenberg et al., 1996]. Changes in the hourly temperatures used by ecosys were interpolated from those in maximum and minimum daily temperatures. These temperature changes resulted in an average cumulative increase of 3.125°C after 100 years which is less than one of 4.5°C under 2 x Ca estimated for western Canada by the Canadian Climate Centre GCM [Boer et al., 1992] but is consistent with one of between 2°C and 3°C estimated under IS92a with aerosol loading by Mitchell et al. [1995]. Because relative humidity was unchanged from that in the control run while temperature rose, atmospheric vapor density also rose as is predicted from increased evaporation rates. Simple increases in precipitation of 0.001 yr⁻¹ were derived from a number of climate simulations using IS92a presented by Kattenberg et al. [1996]. These increases are equivalent to 10% after 100 years which is similar to one of 11% under 2 x Ca estimated for western Canada by the Canadian Climate Centre GCM [Boer et al., 1992]. Solar radiation and wind speed were unchanged from current values. Model results for GPP, NPP, NEP and long-term C accumulation were then compared with those under current climate.

5. Results

5.1. Leaf CO₂ Fixation

Soil C:N ratios of > 50 in the organic layer of the northern old black spruce site (Table 2) limited N mineralization in the model, causing soil mineral N to remain at extremely low concentrations (< 0.2 g NO₃⁻ N m⁻³) during the model run. Large soil C:N ratios are characteristic of boreal coniferous sites [e.g. Mugasha et al., 1991] and are more than double those required for rapid mineralization and uptake of N in forest soils [Troth et al., 1976]. Under these conditions rates of N uptake by root and mycorrhizal surfaces in the model (from parameters in Table 1) were constrained by those of net N mineralization from microbial activity. This constraint on uptake caused large stored C:N ratios to develop in the spruce and moss, which in turn caused leaf C:N ratios in the model to rise from set minimum values given in Table 1. These values resulted in areal N densities in the current year's foliage of 1.5 g N m⁻², which was at the upper end of the range of areal N densities measured at the old black spruce site by Dang et al. [1997].

These activities and densities determined the modeled responses of needle CO₂ fixation to irradiance and C_a shown in Figure 1. The slope of the irradiance response curve at low irradiance (Figure 1a) was determined by the chlorophyll activities and densities, and by the quantum and carboxylation efficiencies used to calculate light reaction rates in the model for which theoretical maxima were used (Table 1). The transition to irradiance-saturated CO₂ fixation at higher irradiance was determined by the specific activities and densities of rubisco used to calculate dark reaction rates in the model (Table 1), and by the shape parameter used in the irradiance response function. This transition occurred in the model at an irradiance of ~300 μmol m⁻² s⁻¹, whereas the measured data indicated a more gradual transition at ~200 μmol m⁻² s⁻¹. The response of CO₂ fixation to rising C_a in the model (Figure 1b) was determined by the activities and densities of rubisco at lower C_a and by those of chlorophyll at higher C_a (Table 1). This response was shaped by the relationship between aqueous CO₂ concentration and the K_m for carboxylation (Table 1) as affected by the K_m for oxygenation and by temperature. The modeled response of CO₂ fixation to rising C_a was independent of the irradiance levels tested at low C_a, but was increasingly constrained by irradiance at higher C_a. The measured response was constrained by irradiance at all C_a.

5.2. Diurnal Mass and Energy Exchange

A transition from clear warm weather (> 25°C) to cool cloudy weather (< 10°C) between June 19 and 20 (DOY 171 and 172 in Figure 2a), accompanied by precipitation (Figure 2b) and soil cooling (Figure 2c), was followed by a transition to clear, cool weather on June 22 (DOY 174 in Figure 2a). The presentation of mass and energy fluxes follows the convention that downward fluxes are positive (i.e. gains to the ecosystem) and upward fluxes are negative (i.e. losses to the ecosystem). Both modeled and measured upward latent heat fluxes remained low (< 200 W m⁻²) through both transitions (Figure 3a). In the model low latent heat fluxes were attributed to low stomatal conductances caused by low CO₂ fluxes (Figure 1) caused in turn
with high irradiance and cool temperatures. Downward fluxes over spruce in the model were larger than those measured under clear weather during this period. Both downward and upward CO₂ fluxes measured and modeled over the moss were about 2 – 3 μmol m⁻² s⁻¹.

A continuous warming from below 20°C to above 25°C occurred under clear (Figure 4a), dry (Figure 4b) conditions from July 25 to 31 (DOY 207 to 213). There was some evidence that ẁ was underestimated by the model. However, the ratio of simulated ẁ to total shortwave radiation provided from the gridded dataset was the same as that measured over boreal coniferous forests by Kaminsky and Dubayah [1997], suggesting that the radiative transfer algorithms in the model were not in error. This warming caused only a small rise in upward latent heat flux from 150 to 200 W m⁻² (Figure 5a), indicating continuing stomatal constraints that caused net radiation to be dissipated mostly as sensible heat. Warming of the air (Figure 4a) and soil (Figure 4b) caused downward CO₂ fluxes measured and modeled over the spruce to decline below 5 μmol m⁻² s⁻¹ and upward CO₂ fluxes to rise above 5 μmol m⁻² s⁻¹, indicating a decline in daily NEP with warming. During this period downward and upward CO₂ fluxes measured and modeled over the moss were comparable, indicating an approximate C balance on a daily basis.

A continuous cooling from above 25°C to below 15°C (Figure 6a) occurred under dry conditions (Figure 6b) between August 30 and September 5 (DOY 243 to 249). Upward latent heat fluxes declined to < 100 W m⁻² during this period, so that changes in net radiation were almost entirely offset by changes in sensible heat (Figure 7a). Downward CO₂ fluxes remained above 5 μmol m⁻² s⁻¹ while upward CO₂ fluxes declined below 5 μmol m⁻² s⁻¹ (Figure 7b), indicating a rise in daily NEP with cooling. With shortening daylengths in early September, the duration of downward CO₂ fluxes measured and modeled within each day was less than that in June (Figure 3b) and July (Figure 5b). Both downward and upward CO₂ fluxes measured and modeled over moss were about 2 μmol m⁻² s⁻¹ (Figure 7b). Other comparisons of modeled versus measured fluxes of CO₂ and water are given by Amthor et al. [this issue].

5.3. Daily C and Water Exchange

Daily totals of NEP measured over spruce during 1996 indicated losses of 0.3 to 0.6 g C m⁻² d⁻¹ until mid-May followed by gains that rose to 2 – 3 g C m⁻² d⁻¹ by late June, after which gains declined to near zero by late September (Figure 8a). Modeled NEP followed the same trend, although peak rates during late May and early June were higher than those measured by about 1 g C m⁻² d⁻¹. Both modeled and measured NEP showed large day-to-day variation. In the model, much of this variation was attributed to short-term changes in weather. The rapid transition from negative NEP on DOY 172 and 173 to large positive NEP on days 174 and 175 (Figure 8a) was attributed to a rise in radiation without a rise in air and soil temperature (Figure 2a, c) that raised GPP without raising ẁ and ẁ (Figure 3b). The transition from positive to negative NEP between DOY 206 and 213 (Figure 8) was attributed to rising air and soil temperatures (Figure 4a, c) that raised ẁ and ẁ more than GPP (Figure 5b). The transition from negative to positive NEP between DOY 242 and 248 (Figure 6a, c) that reduced ẁ and ẁ more than GPP (Figure 7b). The relationship between daily NEP measured and modeled during 1996 is shown in Figure 8b. A statistical

Figure 1. Simulated (lines) and measured (symbols) responses of CO₂ fixation by needles in the upper part of a spruce canopy to changes in (a) irradiance (Cₐ = 360 μmol mol⁻¹, Tₐ = 20 °C, Hₐ = 0.6) and (b) CO₂ concentration (I = 2350 μmol m⁻² s⁻¹, Tₐ = 23.5 °C, RH = 0.5, and I = 650 μmol m⁻² s⁻¹, Tₐ = 20.0 °C, Hₐ = 0.3).
Figure 2. (a) Air temperature, radiation (b) precipitation, wind speed and (c) soil temperatures simulated (lines) and measured (symbols) at the northern old black spruce site from June 18 to 24 (DOY 170 to 176), 1996.

Figure 3. (a) Energy fluxes over black spruce and (b) CO₂ fluxes over black spruce and moss simulated (lines) and measured (symbols) at the northern old black spruce site from June 18 to 24 (DOY 170 to 176), 1996.
analysis of modeled versus measured daily NEP and evapotranspiration is given by Amthor et al. [this issue].

5.4. Annual C Exchange

Total ecosystem GPP modeled in 1994 of 803 g C m\(^{-2}\) (Table 3) was lower than that estimated from respiration chambers by Ryan et al. [1997] but was close to that estimated from eddy correlation fluxes by Goulden et al. [1997]. Spruce and moss GPP accounted for 624 g C m\(^{-2}\) (0.78) and 179 g C m\(^{-2}\) (0.22) respectively of this total. In comparison, Goulden and Crill [1997] estimated from flux measurements made with automated chambers and eddy correlation that moss accounted for 0.1 to 0.5 of total C fixation at this site. Autotrophic respiration in the model accounted for 0.64 and 0.60 of spruce and moss GPP respectively, leaving a total ecosystem NPP of 228 (spruce) + 71 (moss) = 299 g C m\(^{-2}\). This NPP was larger than estimates of 219 and 252 g C m\(^{-2}\) by Gower et al. [1997, Steele et al. [1997] and Ryan et al. [1997] from allometry, litterfall, minirhizotrons and respiration flux chambers. These field estimates attributed only 10 g C m\(^{-2}\) of ecosystem NPP to moss, even though measurements of CO\(_2\) fluxes by Goulden and Crill [1997] and of C storage by Harden et al. [1997] suggested that moss NPP was larger (e.g. Figs. 3b, 5b and 7b). Losses of C from senescence and root exudation in the model left a net biomass growth for spruce of 23 g C m\(^{-2}\) which was less than one of 78 g C m\(^{-2}\) estimated from allometric measurements by Gower et al. [1997], but consistent with growth rates of 20 g C m\(^{-2}\) yr\(^{-1}\) calculated by the Alberta Forest Service [1985] for black spruce trees of the climatic zone, age, height and diameter reported by Gower et al. [1997] from the old black spruce site.

Losses of 245 g C m\(^{-2}\) from heterotrophic respiration in the model left an annual NEP during 1994 of 54 g C m\(^{-2}\) (Table 3), of which 21 and 33 g C m\(^{-2}\) were attributed to gains in plant and soil C respectively. Weather during 1995 and 1996 was cooler and rainier than that during 1994 (average temperature and total precipitation in 1994, 1995 and 1996 were -2.07 °C, -2.55°C and -3.05°C, and 383 mm, 434 mm and 456 mm respectively). Cooler temperatures caused reductions in modeled GPP during 1995 and 1996 versus 1994 that were smaller than those in R\(_a\) + R\(_h\), so that NEP rose to 67 and 60 g C m\(^{-2}\) in 1995 and 1996 from 54 g C m\(^{-2}\) in 1994. These changes in GPP and NEP with changes in climate follow from those modeled under short term changes in temperature (Figs. 3b, 5b and 7b). Gains in ecosystem C modeled during 1995 and 1996 were partitioned mostly to spruce wood. Amthor et al. [this issue] give a summary of the annual C and water balances estimated from eddy correlation fluxes measured between 1994 and 1996, and an analysis of the extent to which they corroborate model results.

After 150 years under the IS92a climate change scenario, C\(_a\) reached 1030 µmol mol\(^{-1}\), maximum and minimum air temperatures had risen by 3.2°C and 4.4°C, and annual precipitation had risen by 65 mm. Higher C\(_a\) raised GPP in the model (Table 3) by raising CO\(_2\) fixation rates (Figure 1b), and higher temperatures raised GPP further by extending the length...
of the growing season within which CO₂ fixation occurred. However the rise in GPP was constrained in the model by N availability that caused foliar biomass and N concentrations to be reduced from current values. Higher air temperatures increased $R_a$ comparatively more than GPP (e.g. Figure 5b) so that NPP rose only marginally from current values. Higher air temperatures caused higher soil temperatures with a longer period and greater depth of topsoil thawing, which increased $R_h$ during the first 75 years of climate change. However after 150 years of climate change declining foliar biomass and N concentrations in the model caused lower soil C and N inputs that limited $R_h$. The modeled rise in NEP under climate change (112 versus 60 g C m⁻² yr⁻¹) was entirely attributed to more rapid spruce growth (125 versus 46 g C m⁻² yr⁻¹). This rise was partly an artifact of modeled spruce senescence, which sometimes alternated between lower and higher values during successive years so that annual rises in spruce growth under climate change alternated about a longer term mean. Climate change caused the soil to become a net C source (-10 g C m⁻² yr⁻¹).

5.5. Long-Term C Accumulation

Annual values of NEP in the model (e.g. Table 3) were influenced by antecedent C stored in the spruce, moss and forest floor as affected by antecedent climate through its different effects on GPP, $R_a$ and hence litterfall. More definitive estimates of annual NEP in this forest should therefore be derived from values simulated over several years. When run over a 150 year period, the model indicated very slow wood C accumulation during the first 75 years after seeding because N and P were sequestered by C turnover in moss (Figure 9a) which developed a C:N ratio of about 30. After 75 years the modeled spruce fully shaded the moss, reducing moss C turnover and N and P sequestration, so that more N and P became available for spruce growth. Spruce wood C then accumulated at a stable rate of 42 g C m⁻² yr⁻¹. Wood C accumulation in the model is close to that derived from allometric equations for wood growth of black spruce for the site productivity index (fair) indicated by the age and height of the spruce trees at the experimental site (Alberta Forest Service, 1985) (Figure 9a). Early accumulation in the model was strongly affected by the competitive environment for nutrient acquisition provided by the moss. Total C accumulation modeled in wood, foliage and living moss after 150 years (4237, 381 and 19 g C m⁻²) was less than that measured by Gower et al. [1997] (4300, 500 and 60 g C m⁻²), but rising.

Soil C declined during the first 50 years of the model run while most C turnover occurred through moss, and then accumulated at a rate of 15 g C m⁻² yr⁻¹ for the next 100 years as spruce became the dominant source of litterfall (Figure 9b). Nakane et al. [1997] estimated soil C accumulations of 3 to 13 g C m⁻² yr⁻¹ from measurements of litterfall and soil respiration between June 1994 and May 1995 at the southern old black spruce site. Harden et al. [1997] estimated a net soil sequestration rate of 10 to 30 g C m⁻² yr⁻¹ from soil C accumulation at the northern old black spruce site, although Goulden et al. [1998] estimated a net soil loss of 80 g C m⁻² yr⁻¹ from eddy correlation fluxes measured in 1994.

Climate change raised wood C accumulation in the model to double its value under current climate after 150 years (Figure 9a). Total wood C accumulation in the model was comparable to one of 8350 g C m⁻² derived from allometric equations for wood
growth of black spruce under current climate at a site with a good productivity index (the best index used by the Alberta Forest Service, 1985). Soil C under climate change declined and recovered more rapidly than did that under current climate during the first 60 years of the model run (Figure 9b). However soil C did not continue to accumulate after 60 years under climate change, and started to decline after 130 years, whereas soil C accumulated steadily after 60 years under current climate.

6. Discussion

Mass and energy exchanges over black spruce forests are characterized by low CO2 fixation rates and high Bowen ratios (Figs. 3a, 5a and 7a) even though these exchanges are not limited by soil water. These high ratios indicate a stomatal constraint to latent heat flux that might be caused by an environmental constraint to CO2 fixation. Modeled CO2 fixation in black spruce was strongly constrained by high stored C:N ratios in leaves that reduced the specific activities (Figure 1) and surface densities of leaf chlorophyll and rubisco to half of maximum values set from fertilization experiments (Table 1). These high C:N ratios occurred in the model because plant N uptake was limited by extremely low NH4+ and NO3- concentrations in the soil solution of the rooting zone. These low concentrations arose in the model from the slow mineralization of spruce detritus caused by their comparatively high lignin concentrations [Trofymow et al. 1995] (Table 1), and from the slow mineralization of soil organic matter caused by its high soil C:N ratios (Table 2). Mineralization of plant detritus and soil organic matter was further slowed in the model by low specific microbial activity caused by low soil temperatures that developed under the large surface detritus (~400 g C m^-2 in the model which was also measured at most of the black spruce sites sampled by Halliwell et al., 1995) that accumulated under the spruce and the moss. Reduced microbial activity was apparent in the low R_h modeled at the northern old black spruce site (245 g C m^-2 yr^-1 in Table 3). Low microbial activity in the model under spruce also resulted in low rates of N2 fixation (ca. 0.5 g N m^-2 yr^-1 under spruce versus 2.5 g N m^-2 yr^-1 under aspen where modeled R_h = 525 g C m^-2 yr^-1 in Grant et al., 1999a) that also contributed to low soil NH4+ and NO3- concentrations. These modeled fixation rates are within the ranges of 0.03 to 1.85 g N m^-2 yr^-1 and 0.35 to 3.25 g N m^-2 yr^-1 measured in soils under black spruce and aspen respectively by Brouzes et al. [1969]. Furthermore low pH (Table 1) reduced soluble P concentrations in the model [Grant and Heaney, 1997] and hence P uptake, growth and activity by both microbial and plant populations (notably moss, which developed roots only within the low pH zone in the upper 0.15 m of the soil profile).

Low CO2 fixation rates caused by high C:N ratios forced low stomatal conductances in the model, based on the assumed conservation of the C_l/C_a ratio. Low conductances in black spruce (typically 0.02 – 0.04 mol CO2 m^-2 s^-1 under full sunlight) were inferred from leaf chamber and C isotope
Figure 7. (a) Energy fluxes over black spruce and (b) CO₂ fluxes over black spruce and moss simulated (lines) and measured (symbols) at the northern old black spruce site from August 30 to September 5 (DOY 243 to 249), 1996.

Figure 8. (a) Daily net ecosystem productivity (NEP) simulated (line) and measured (symbols), and (b) simulated versus observed NEP at the northern old black spruce site during 1996.
discrimination studies by Flanagan et al. [1997] and measured
with a portable photosynthesis system by Middleton et al. [1997].
These low conductances caused the small latent heat fluxes and
large sensible heat fluxes modeled in Figs. 3a, 5a and 7a. Because
the response of CO2 fixation (Figure 1a) to irradiance above 500
µmol m⁻² s⁻¹ was limited, increases in net radiation were mostly
offset by increases in sensible heat flux. Such increases were
apparent in the field data, and have also been reported from eddy
correlation measurements at the southern old black spruce site by
Jarvis et al. [1997] and Pattey et al. [1997].
Small latent heat fluxes in the model caused low rates of
water uptake from the soil, leading to periodic saturation, runoff
and discharge (about 100 mm yr⁻¹). Surface water accumulation
and high soil water contents were observed at the old black
spruce site during much of 1994 [Peck et al., 1997]. Wet soil
further slowed mineralization of plant detritus and soil organic
matter in the model because consequent low soil O2
concentrations occasionally reduced energy yields from microbial
activity [Grant, 1998b; Grant and Pattey, 1999] (Table 2). Low
soil temperatures and O2 concentrations also strongly constrained
root growth [Grant, 1993a] below 0.35 m in the model, limiting
plant access to deeper soil nutrients. Poor soil drainage has been
directly linked to low foliar N concentrations and low growth
rates of black spruce in Canadian boreal forests [Liefers and
Macdonald, 1990].
The low soil nutrient content at the old black spruce site thus
caused a series of self-reinforcing processes in ecosys (low
nutrient and high lignin content in spruce detritus → slow
detritus decomposition → slow nutrient mineralization and
biological N fixation → surface detritus accumulation → cold soil
→ slow nutrient mineralization and biological N fixation → slow
nutrient uptake → low CO2 fixation → low transpiration → wet
soil → slow detritus decomposition → slow nutrient
mineralization and biological N fixation ...) that caused NPP and
NEP to stabilize at low values (Table 3; Figure 9) in comparison
to deciduous ecosystems in the same climate [Grant et al.,
1999a]. Soil warming under the IS92a climate change scenario
casted a series of changes in these processes (warmer soil →
faster detritus decomposition → faster nutrient mineralization
and biological N fixation → slower surface detritus
accumulation → warmer soil → faster nutrient mineralization and
biological N fixation → faster nutrient uptake → higher CO2
fixation → faster detritus deposition → faster detritus
decomposition → faster nutrient mineralization and biological N
fixation ...) that caused NPP and NEP to rise over time. These
changes with soil warming under IS92a were magnified by the
earlier and deeper descent of the thawing front modeled during
June and July.
The modeled spruce/moss forest remained a stable net sink
for atmospheric C of about 40 (wood) + 15 (soil) = 55 g C m⁻²
yr⁻¹ (Figure 9), largely because soil C oxidation was constrained
in the model by the chemical composition of the detritus, and by
the low nutrient, heat and periodically the low O2 contents of the
soil. The modeled soil C sink is consistent with that estimated by
Nakane et al. [1997] and Harden et al. [1997]. The modeled
wood C sink is consistent with a long-term average wood growth
rate of 30 to 40 g C m⁻² yr⁻¹ estimated from aboveground
measurements of ecosystem C at the northern old black spruce
site by Gower et al. [1997]. It is also consistent with wood
growth rates estimated by the Alberta Forest Service [1985] at
fair to medium sites under climates comparable to that at the
northern old black spruce site (Figure 9). These measured and
modeled rates of soil and wood C accumulation suggest a NEP of
50 to 60 g C m⁻² yr⁻¹ by the spruce/moss forest at this low-
productivity site in the northern study area of BOREAS. This rate
is less than that one of 100 (wood) + 30 (soil) g C m⁻² yr⁻¹

Figure 9. (a) Spruce wood C and (b) soil organic C simulated at the northern old black spruce site during 150 years
under current (1994 -1996) and hypothesized climates (lines), and (a) spruce wood C at fair and medium sites
calculated from wood volume measurements by the Alberta Forest Service [(1985] (symbols).
simulated [Grant et al., 1999a] and measured [Black et al., 1996] at the southern old aspen site where rates of C cycling were larger. It is also less than the 60 (wood) + 10 (soil) g C m^{-2} yr^{-1} simulated [Grant et al., 2001] and measured [Jarvis et al., 1997] at the southern old black spruce site. Both these southern sites have mean annual temperatures ~2°C higher than that at the northern site simulated here. However if applied to the entire boreal forest zone, the NEP estimated at the northern old black spruce site would account for a global sink of 1 Gt C yr^{-1} [Sellers et al., 1997]. Enhancement of this sink would require an improvement in the nutrient status of boreal black spruce forests, as might occur if atmospheric N deposition rates were to rise. Grant et al. [2001] used ecosys to predict a substantial increase in wood C accumulation over 150 years by a black spruce stand in the southern study area of BOREAS under the IS92a climate change scenario should mineral N concentration in precipitation rise from 0.5 to 2.0 g N m^{-3}.

Rising C and air temperatures hypothesized under the IS92a climate change scenario are predicted by ecosys to cause a gain of 5000 g C m^{-2} by a boreal spruce-moss ecosystem after 150 years. However this gain would include a gain of 5700 g C m^{-2} in spruce wood and a loss of 700 g C m^{-2} in soil organic matter. These gains in wood C would be vulnerable to loss by fire and insects which are important natural disturbances in boreal ecosystems. The frequency of these disturbances may increase under a warmer climate, especially if increases in precipitation do not accompany those in temperature.

References


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