



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

Controls on carbon and energy exchange by a black spruce - moss ecosystem: Testing the mathematical model Ecosys with data from the BOREAS experiment

Citation for published version:

Grant, RF, Jarvis, PG, Massheder, JM, Hale, SE, Moncrieff, JB, Rayment, M, Scott, SL & Berry, JA 2001, 'Controls on carbon and energy exchange by a black spruce - moss ecosystem: Testing the mathematical model Ecosys with data from the BOREAS experiment', *Global Biogeochemical Cycles*, vol. 15, no. 1, pp. 129-147. <https://doi.org/10.1029/2000GB001306>

Digital Object Identifier (DOI):

[10.1029/2000GB001306](https://doi.org/10.1029/2000GB001306)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Global Biogeochemical Cycles

Publisher Rights Statement:

Published in Global Biogeochemical Cycles by the American Geophysical Union (2001)

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



Controls on carbon and energy exchange by a black spruce – moss ecosystem: Testing the mathematical model *Ecosys* with data from the BOREAS experiment

R. F. Grant

Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada

P.G. Jarvis, J.M. Massheder, S.E. Hale, J.B. Moncrieff, M. Rayment, and S.L. Scott

Institute of Ecology and Resource Management, University of Edinburgh, Edinburgh, Scotland

J.A. Berry

Department of Plant Biology, Carnegie Institution of Washington, Stanford, California

Abstract. Stomatal limitations to mass and energy exchange over boreal black spruce forests may be caused by low needle N concentrations that limit CO₂ fixation rates. These low concentrations may be caused by low N uptake rates from cold boreal soils with high soil C:N ratios and by low N deposition rates from boreal atmospheres. A mathematical model of terrestrial ecosystems *ecosys* was used to examine the likelihood that slow N cycling could account for the low rates of mass and energy exchange measured over a 115-year old boreal spruce/moss forest as part of the Boreal Ecosystem-Atmosphere Study (BOREAS). In the model, net N mineralization was slowed by the high C:N ratios measured in the forest floor and by high lignin contents in spruce litterfall. Slow mineralization caused low N uptake rates and hence high C:N ratios in spruce and moss leaves that reduced specific activities and areal densities of rubisco and chlorophyll. Consequent low CO₂ fixation rates caused low stomatal conductances and transpiration rates which in turn caused high soil water contents. Wet soils, in conjunction with large accumulations of surface detritus generated by slow litter mineralization, caused low soil temperatures that further slowed mineralization rates. Model outputs for ecosystem N status were corroborated by low needle N concentrations ($< 10 \text{ mg g}^{-1}$), stomatal conductances ($< 0.05 \text{ mol m}^{-2} \text{ s}^{-1}$) and CO₂ fixation rates ($< 6 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$), and by high canopy Bowen ratios (1.5–2.0) and low canopy net CO₂ exchange rates ($< 10 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) measured over the black spruce/moss forest at the BOREAS site. Modeled C accumulation rates of 60 (wood) + 10 (soil) = 70 g C m⁻² yr⁻¹ were consistent with estimates from aggregated CO₂ fluxes measured over the spruce canopy and from allometric equations developed for black spruce in Canadian boreal forests. Model projections under IS92a climate change indicate that rates of wood C accumulation would rise and those of soil C accumulation would decline from those under current climate. Because these rates are N-limited, they would be raised by increases in atmospheric N deposition.

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 ecosystem productivity (NEP) of these forests will be affected by rising temperatures and atmospheric CO₂ concentrations (C_a). Boreal coniferous forests are currently thought to be sinks for atmospheric CO₂ [Sellers *et al.*, 1997] based on seasonal variation and isotopic analyses of C_a [e.g. Ciais *et al.*, 1995;

Keeling *et al.*, 1995]. However midday evaporative fractions and CO₂ fluxes measured by Jarvis *et al.* [1997] and Pattey *et al.* [1997] over a black spruce stand in the southern study area of the Boreal Ecosystem-Atmosphere Study (BOREAS) were only 0.35–0.45 and 6–9 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ respectively, indicating a stomatal limitation to transpiration and CO₂ fixation. This limitation was apparent in the low stomatal conductances of black spruce needles (0.025–0.035 $\text{mol m}^{-2} \text{ s}^{-1}$) measured by Middleton *et al.* [1997] in the same stand. Soil moisture measurements in the same stand by Peck *et al.* [1997] indicate that the stomatal limitation to mass exchange by black spruce forests was not likely due to soil water deficits.

Based on the correspondence between low CO₂ fixation rates and low N concentrations of black spruce needles reported by Middleton *et al.* [1997], this stomatal limitation was likely caused by N deficits. Such deficits were apparent in the > 40% increases of needle N concentration and growth measured by

Copyright 2001 by the American Geophysical Union.

Paper number 2000GB001306.
0886-6236/01/2000GB001306\$12.00

Mugasha *et al.* [1991] following N fertilization of black spruce at a site in Alberta with a stand density, growth rate, soil C:N ratio and foliar N concentration similar to those at the BOREAS site. Nitrogen deficits at these sites arise from C:N ratios in the soil organic layer that are double those of 19 to 27:1 required for rapid mineralization and uptake of N in forest soils [Troth *et al.*, 1976]. Mineralization and uptake of N are further constrained by low soil temperature and aeration [e.g. Campbell, 1980; Lieffers and Rothwell, 1987] caused by poor drainage and thermal insulation by moss.

A key objective of BOREAS is to improve our understanding of mass and energy exchange between boreal forest ecosystems and the atmosphere by collecting data at temporal and spatial scales appropriate to well constrained tests of process-based ecosystem models [Sellers *et al.*, 1997]. If these tests are successful, then the confidence with which such models may be used to predict changes in mass and energy exchange under changing climates would be greatly improved. One ecosystem model included in these tests is *ecosys* [Grant, 1996a, b], output from which has been compared in an earlier study with measurements of diurnal mass and energy exchange and of long term C accumulation in a boreal deciduous forest at the southern old aspen site [Grant *et al.*, 1999a]. This model simulates transformations and transfers of C, N and P in soils and plants as affected by soil temperature [Grant, 1993a; 1994b; Grant *et al.*, 1993a, b; Grant and Rochette, 1994; Grant *et al.*, 1995a], water content [Grant *et al.*, 1993a, b; Grant and Rochette, 1994] and aeration [Grant, 1993b; 1995; Grant *et al.*, 1993c, d; Grant and Pattey, 1999]. In the model, low net mineralization rates may constrain N uptake rates through plant roots which may cause low concentrations of N and P in plant leaves. These low concentrations may limit specific activities and densities of leaf rubisco and chlorophyll, thereby constraining leaf CO₂ fixation and stomatal conductance, and hence canopy mass and energy exchange. This model is thus well suited to test the hypothesis that low rates of N mineralization in soils under boreal coniferous forests cause N limitations on leaf carboxylation activity that result in the low rates of canopy CO₂ fixation and transpiration measured at boreal coniferous sites. This hypothesis was tested by comparing results for mass and energy exchange from the model with those reported by Jarvis *et al.* [1997] from the old black spruce site in the southern study area of BOREAS. The model was then used to simulate changes in long-term C accumulation at the old black spruce site under changes in C_a, precipitation and temperature hypothesized for the IS92a emissions scenario.

2. Model Development

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, defined by height, azimuth and inclination, of multispecific plant canopies 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, temperature and CO₂ concentration. 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 [Grant *et al.*, 1999b] generated from a convergence solution for canopy water potential at which the difference between transpiration and root water uptake [Grant *et al.*, 1999b] equals the difference between canopy water contents at previous and current water potentials. Canopy transpiration is solved from a first order solution to the canopy energy balance of each plant species [Grant *et al.*, 1999b].

2.1.2. Autotrophic Respiration and Senescence. The product of CO₂ fixation is added to a C storage pool for each branch of each plant species from which C is oxidized to meet maintenance respiration requirements using a first order function of storage C [Grant *et al.*, 1999b]. If the C storage pool 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 2.2.1. Environmental constraints such as nutrient, heat or water stress that reduce net C fixation and hence C storage will therefore accelerate litterfall. When storage C oxidation 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 [Itoh and Barber, 1983] given by a root and mycorrhizal growth submodel [Grant, 1993a, b; 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 root and mycorrhizal C, N and P storage [Grant, 1998b]. The products of N and P uptake are added to root and mycorrhizal storage pools from which they are combined with storage 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 N₂ is reduced to storage N through oxidation of storage C according to the energetics in Schubert [1982]. This reduction generates concentration gradients of

storage 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 storage 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 storage C, N and P in each root zone of each plant species [Grant, 1993a, b; 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 storage C, N and P among branches, roots and mycorrhizae. These transfers are driven from concentration gradients within the plant that develop from different rates of C, N or P acquisition and consumption by its branches, roots or mycorrhizae [Grant, 1998b]. When root N or P uptake rates described in section 2.1.3 are low, storage N or P concentrations in roots and branches become low with respect to those of storage C. Such low ratios in branches reduce the specific activities and surficial concentrations of leaf rubisco and chlorophyll which in turn reduce leaf CO_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 storage 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].

For perennial nonconiferous plant species, soluble C, N and P are withdrawn from storage pools in branches into a long-term storage pool in the crown during autumn, causing leaf senescence. Soluble C, N and P are remobilized from this pool to drive leaf and petiole or sheath growth the following spring. The timing of withdrawal and remobilization is determined by duration of exposure to low temperatures (between 3°C and 8°C) under shortening and lengthening photoperiods respectively.

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 nonparticulate 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 type including obligate aerobes, facultative anaerobes (denitrifiers), obligate anaerobes (fermenters), methanogens and diazotrophs.

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 spatially resolved soil profile [Grant, 1997; Grant and Rochette, 1994; Grant et al., 1998]. A fraction of the hydrolysis products of lignin are 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_2 emission from the soil surface. This oxidation is coupled to the reduction of O_2 by all aerobic populations [Grant et al., 1993a, b; Grant and Rochette, 1994], to the sequential reduction of NO_3^- , NO_2^- and N_2O 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_4^+ and NO_2^- oxidation [Grant, 1994a] and N_2O evolution [Grant, 1995], and autotrophic methanotrophs conduct CH_4 oxidation [Grant, 1999], the energetics of which determine autotrophic growth yields and hence biomass and activity. Microbial populations in the model seek to maintain steady-state ratios of biomass C:N:P by mineralizing or immobilizing NH_4^+ , NO_3^- and H_2PO_4^- , 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, b]. 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 southern study area of BOREAS (53.99°N, 105.19°W) is almost flat, poorly drained, and covered by a dominant canopy of black spruce (*Picea mariana* (Mill.) BSP), age 115 years, height 7.2 m, density 5990 ha^{-1} from Gower et al., 1997) with some jack pine (*Pinus banksiana*) and tamarack (*Larix laricina* (Du Roi) K. Koch) in

Table 1. Physical and Biological Properties of the Cumic Humic Regosol at the Southern Old Black Spruce Site [Anderson, D. 1998, BOREAS TE-01 Soils Data over the SSA Tower Sites in Raster Format, Available online at [http://www-eosdis.ornl.gov/] from the ORNL Distributed Active Archive Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee, U.S.A.]

Depth, m	0.01	0.05	0.15	0.30	0.35	0.47	0.72	0.96	1.20
BD [†] , Mg m ⁻³	0.10	0.10	0.10	0.10	1.25	1.52	1.66	1.66	1.66
$\theta_{-0.03\text{MPa}}$, m ³ m ⁻³	0.40	0.40	0.40	0.40	0.218	0.213	0.183	0.022	0.034
$\theta_{-1.5\text{MPa}}$, m ³ m ⁻³	0.20	0.20	0.20	0.20	0.056	0.049	0.050	0.012	0.013
Sand, kg kg ⁻¹	0	0	0	0	756	728	646	960	949
Silt, kg kg ⁻¹	0	0	0	0	200	214	287	19	30
pH	3.4	3.4	3.4	3.4	4.3	4.3	4.9	5.8	6.6
CEC, cmol kg ⁻¹	75.8	75.8	75.8	75.8	9.0	10.1	8.2	2.9	2.5
Org. C, g kg ⁻¹	434	434	434	434	11.4	9.8	3.6	1.0	0.5
Org. N, mg kg ⁻¹	8162	8162	8162	8162	603	423	215	52	52
Org. P, mg kg ⁻¹	900	900	900	900	75	53	27	7	7
Al-P, mg kg ⁻¹	0	0	0	0	164	225	192	149	183
Ca-P, mg kg ⁻¹	0	0	0	0	0	0	100	150	200

[†] abbreviations are as follows: BD, bulk density; θ , water content; CEC, cation exchange capacity; Al-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.

better drained locations. The site has a sparse shrub layer underlain by moss hummocks consisting of *Sphagnum* spp. and *Pleurozium schreberi* with *Hylocomium splendens* in poorer and better drained locations respectively. A slight slope from north to south allows run off of surface water. 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 CO₂ Fixation

On August 28, 1994 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 mirror (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, leaf temperature or CO₂ with all other environmental conditions held constant. Response of CO₂ flux to changes of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in irradiance was measured at a CO₂ concentration of 355 $\mu\text{mol mol}^{-1}$, a leaf temperature of 15°C, and a vapor pressure of 1.3 kPa. Response of CO₂ flux to 2.5°C changes in leaf temperature was measured at a CO₂ concentration of 345 $\mu\text{mol mol}^{-1}$, an irradiance of 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and a vapor pressure that increased with air temperature from 1.1 kPa at 12°C to 2.0 kPa at 35°C. Response of CO₂ flux to 50 – 100 $\mu\text{mol mol}^{-1}$ changes in CO₂ concentration was measured at an irradiance of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, a leaf temperature of 11°C and a vapor pressure of 1.0 kPa. Measurements of CO₂ flux and stomatal conductance were taken once steady state values were achieved (usually 30 min after conditions were changed).

3.3. Canopy Mass and Energy Exchange

Mass and energy exchange were measured continuously between May 23 and September 21, 1994 over a 26-m flux tower using an eddy correlation system consisting of a triaxial sonic

anemometer (Solent, Gill Instruments Limited, Lymington, United Kingdom) and a closed-path infrared gas analyzer (IRGA) (LI-6262, LI-COR, Lincoln, Nebraska). The anemometer was mounted on a vertical pole 2.6 m above the SW corner of the top platform of the tower. Air 5 cm from the center of the sonic anemometer's path was ducted down a 32-m 6 mm ID heated tube (Dekabon 13, J.P. Deane & Co. Ltd., Glasgow, United Kingdom) at 6 dm³ min⁻¹ (Tylan FC2900B mass flow controller, Swindon, United Kingdom), which caused pressure in the IRGA sample cell to be typically 7 kPa less than atmospheric. Half-hourly averages of CO₂, and latent and sensible heat fluxes were calculated using the EdiSol system [Moncrieff *et al.*, 1997]. During each flux-averaging period, EdiSol collected 20 readings per second of wind speed components, speed of sound, and concentrations of CO₂ and water vapor. A digital recursive 200 s running mean was used with each reading to calculate fluctuations and their covariances with vertical wind speed. At the end of each period, coordinate rotation of the wind vector components was used to eliminate contamination of vertical wind fluxes by horizontal wind flow. Calculated travel times from the above-canopy sensors were then used to select the covariances used in the flux calculations. Cospectra for water vapor and CO₂ fluxes were compared with the cospectrum for heat flux measured at the sonic anemometer to correct for attenuation of the high frequency component during travel to the ground-based detectors. Net radiation (2 Q-6 net radiometers, REBS, Seattle, Washington) was measured at a height of 18 m on the southern side of the flux tower. Soil heat flux was measured with an array of seven heat flux plates (HFT-3, Campbell Scientific, United Kingdom) buried 2 cm below the soil surface. Vertical profiles of CO₂ concentration were measured at heights of 1.5, 3, 6, 12 and 26 m with 4 mm ID nylon tubes through which air was drawn at 1 dm³ min⁻¹ to an IRGA (ADC 225, Analytical Development Co. Ltd. Hoddeston, United Kingdom) fitted with time-switched solenoid valves set to a 15-min cycle. Changes in half-hourly mean concentrations were integrated vertically to calculate canopy CO₂ storage fluxes. Further details of canopy mass and energy exchange measurements are given by Jarvis *et al.* [1997].

4. Model Experiment

4.1. Model Initialization and Run

The ecosystem model *ecosys* was initialized with data for the physical properties of the Cumic Humic Regosol at the southern black spruce site of BOREAS [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 maximum leaf N:C ratio was reduced from 0.15 g g⁻¹ for broadleaf plants to 0.05 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 N:C ratios decline below this maximum value if N limits plant growth. (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]. Coefficients for photosynthetically active radiation 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 2).

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 moss relative humidity according to data given by *Proctor* [1982] and by *Clymo and Hayward* [1982], rather than from stomatal resistance and water potential as in vascular plants.

The biochemical composition of moss litter is currently assumed to be the same as that of deciduous vegetation, although some compounds produced by moss may slow decomposition. 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., 1993e; 1995b; 1999b], forests [Grant et al., 1999a] and soils [Grant, 1994a; 1997; Grant and Rochette, 1994; Grant et al., 1993a, b, c, d; 1995a; 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 recorded in the coniferous zone of the BOREAS southern study area during 1994, 1995 and 1996 by the Saskatchewan Research Council and compiled for modeling purposes by BOREAS staff. Model C_a was initialized at 294 $\mu\text{mol mol}^{-1}$ and incremented daily at a rate of 0.00167 yr⁻¹ so that C_a recorded in 1994 would be reached after 115 years. Atmospheric N deposition in the model occurred as NH₄⁺ and NO₃⁻ dissolved in precipitation (0.25 g N m⁻³ of each) and as NH₄⁺ from adsorption of atmospheric NH₃ (0.004 $\mu\text{mol mol}^{-1}$). 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. These populations remained constant during the model run as mortality of individual plants is not yet simulated. No other interventions occurred during the entire run.

To test model sensitivity to gradual changes in atmospheric boundary conditions, the model was run for 150 years as described above, but C_a was initialized at 360 $\mu\text{mol mol}^{-1}$ and C_a , temperature and precipitation were incremented daily from recorded values at rates derived from the IS92a emissions scenario in *Kattenberg et al.* [1996] (Table 3). To test model sensitivity to increases in atmospheric N deposition, the same run was made with concentrations of NH₄⁺ and NO₃⁻ in precipitation raised from 0.25 to 1.0 g N m⁻³ of each.

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 28 in the 115th year of the model run during which 1994 meteorological data had been used. The model was then run for 24 hours under incremental changes in irradiance, leaf temperature or C_a with all other environmental conditions maintained at values used in the leaf CO₂ fixation study described in section 3.2. 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 toward 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. An additional run was conducted under high irradiance (1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$), temperature (27°C), C_a (10⁴ $\mu\text{mol mol}^{-1}$) and vapor pressure (2.2 kPa) to test maximum net CO₂ fixation rates in the model against values measured under these same conditions on needles taken from the old black spruce site by *Middleton et al.* [1997].

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

Table 2. Key Biological Properties of Spruce, Moss and Soil Microbial Populations Used in *Ecosys*.

Variable	Value	Units
<i>Spruce and Moss</i>		
Maximum carboxylation rate	50	$\mu\text{mol CO}_2 \text{ g}^{-1} \text{ rubisco s}^{-1}$ at 30°C
Maximum rubisco oxygenation rate	10.5	$\mu\text{mol O}_2 \text{ g}^{-1} \text{ rubisco s}^{-1}$ at 30°C
Maximum electron transport rate	500	$\mu\text{mol e}^- \text{ g}^{-1} \text{ chlorophyll s}^{-1}$ at 30°C
Quantum efficiency	0.5	$\mu\text{mol e}^- \mu\text{mol quanta}^{-1}$
Michaelis-Menten constant for carboxylation	12.5	$\mu\text{M CO}_2$ at 30°C
Michaelis-Menten constant for oxygenation	500	$\mu\text{M O}_2$
Transmission and reflection of shortwave radiation	0.15	
Transmission and reflection of PAR	0.075	
Fraction of leaf protein in rubisco	0.10 (spruce) 0.25 (moss)	$\text{g (C) g}^{-1} \text{ (C)}$
Fraction of leaf protein in chlorophyll	0.02 (spruce) 0.05 (moss)	$\text{g (C) g}^{-1} \text{ (C)}$
Maximum N:C ratio in leaf	0.05 (spruce) 0.15 (moss)	$\text{g (N) g}^{-1} \text{ (C)}$
N:C ratio in twig and root	0.025	$\text{g (N) g}^{-1} \text{ (C)}$
N:C ratio in stem	0.00375	$\text{g (N) g}^{-1} \text{ (C)}$
Maximum P:C ratio in leaf	0.005 (spruce) 0.015 (moss)	$\text{g (P) g}^{-1} \text{ (C)}$
P:C ratio in twig and root	0.0025	$\text{g (P) g}^{-1} \text{ (C)}$
P:C ratio in stem	0.000375	$\text{g (P) g}^{-1} \text{ (C)}$
Maintenance respiration of plant	0.016	$\text{g (C) g}^{-1} \text{ (N) h}^{-1}$ at 30°C
Growth yield of leaf and twig	0.64	$\text{g (C) g}^{-1} \text{ (C)}$
Growth yield of stem	0.76	$\text{g (C) g}^{-1} \text{ (C)}$
Growth yield of root	0.64	$\text{g (C) g}^{-1} \text{ (C)}$
Interception fraction (spruce)	0.5	$\text{m}^2 \text{ m}^{-2}$
Interception fraction (moss)	1.0	$\text{m}^2 \text{ m}^{-2}$
$C_i:C_a$ ratio at non-limiting water	0.7	
Maximum root NH_4^+ uptake rate	0.025	$\text{g (N) m}^{-2} \text{ root area h}^{-1}$ at 30°C
Michaelis-Menten constant for root NH_4^+ uptake	0.40	g (N) m^{-3}
Minimum NH_4^+ concentration for root uptake	0.03	g (N) m^{-3}
Maximum root PO_4^{2-} uptake rate	0.005	$\text{g (P) m}^{-2} \text{ root area h}^{-1}$ at 30°C
Michaelis-Menten constant for root PO_4^{2-} uptake	0.075	g (P) m^{-3}
Minimum PO_4^{2-} concentration for root uptake	0.002	g (P) m^{-3}
<i>Soil</i>		
Litterfall protein content	0.07 (spruce) 0.07 (moss)	$\text{g (C) g}^{-1} \text{ (C)}$
Litterfall carbohydrate content	0.27 (spruce) 0.34 (moss)	$\text{g (C) g}^{-1} \text{ (C)}$
Litterfall cellulose content	0.36 (spruce) 0.43 (moss)	$\text{g (C) g}^{-1} \text{ (C)}$
Litterfall lignin content	0.30 (spruce) 0.16 (moss)	$\text{g (C) g}^{-1} \text{ (C)}$
Specific activity of protein decomposition	1.0	$\text{g (C) g}^{-1} \text{ microbial (C) h}^{-1}$ at 30°C
Specific activity of carbohydrate decomposition	1.0	$\text{g (C) g}^{-1} \text{ microbial (C) h}^{-1}$ at 30°C
Specific activity of cellulose decomposition	0.15	$\text{g (C) g}^{-1} \text{ microbial (C) h}^{-1}$ at 30°C
Specific activity of lignin decomposition	0.025	$\text{g (C) g}^{-1} \text{ microbial (C) h}^{-1}$ at 30°C
Specific activity of active OM decomposition	0.025	$\text{g (C) g}^{-1} \text{ microbial (C) h}^{-1}$ at 30°C
Specific activity of humus decomposition	0.005	$\text{g (C) g}^{-1} \text{ microbial (C) h}^{-1}$ at 30°C
Specific respiration rate	0.20	$\text{g (C) g}^{-1} \text{ microbial (C) h}^{-1}$ at 30°C
M-M const. for microbial C uptake	35	g (C) m^{-3}
Maintenance respiration of labile biomass	0.010	$\text{g (C) g}^{-1} \text{ microbial (N) h}^{-1}$ at 30°C
Maintenance respiration of resistant biomass	0.0015	$\text{g (C) g}^{-1} \text{ microbial (N) h}^{-1}$ at 30°C
Energy yield of C oxidation with O_2 reduction	37.5	$\text{kJ g}^{-1} \text{ (C)}$
Energy yield of C oxidation with NO_x reduction	10.0	$\text{kJ g}^{-1} \text{ (C)}$
Energy yield of C oxidation with acetate reduction	1.03	$\text{kJ g}^{-1} \text{ (C)}$
Energy requirement for microbial growth	25.0	$\text{kJ g}^{-1} \text{ (C)}$
Requirement of C oxidation for N_2 fixation	6.0	$\text{g (C) g}^{-1} \text{ (N)}$

exchange over the spruce-moss stand simulated under 1994 meteorological data were compared with results obtained from the flux tower at the field site during 1994. Simulated CO_2 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 CO_2 and energy fluxes over the moss were

calculated as the sum of those from the soil surface, the surface detritus and the moss. Three one-week periods were selected for comparison during 1994. The first was in late spring (June 8-14) to observe model behavior during a transition from clear warm weather to cool cloudy weather. The second was in midsummer (July 24-30) to observe model behavior during a period of high

Table 3. Rates of Changes in Atmospheric Boundary Conditions Under Emissions Scenario IS92a

Boundary Condition	Change (y^{-1})			
	Winter	Spring	Summer	Autumn
CO ₂ concentration	+0.007	+0.007	+0.007	+0.007
Maximum daily temperature	+0.030 °C	+0.025 °C	+0.025 °C	+0.030 °C
Minimum daily temperature	+0.040 °C	+0.035 °C	+0.030 °C	+0.035 °C
Precipitation	+0.001	+0.001	+0.001	+0.001
Solar radiation	unchanged	unchanged	unchanged	unchanged
Relative humidity	unchanged	unchanged	unchanged	unchanged
Wind speed	unchanged	unchanged	unchanged	unchanged

and rising temperature and humidity. The third was in late summer (September 7-13) 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 above-ground phytomass growth of a 115-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.

5. Results

5.1. Leaf CO₂ Fixation

On August 28 of the last year of the model run with 1994 climate data, average modeled values for the leaf mass:area ratio and N concentration in current year's foliage of black spruce were 152 g DM m⁻² and 10.8 mg g DM⁻¹. These values compared with average ones of 156 g DM m⁻² and 8.5 mg g DM⁻¹ measured at the southern old black spruce site on July 28 and September 13 1994 by Middleton *et al.* [1997]. Soil C:N ratios of > 50 in the organic layer (Table 1) limited N mineralization in the model, causing soil mineral N to be drawn down to 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 2) were constrained by those of N mineralization from microbial activity. This constraint on uptake caused low storage N:C ratios to develop in the spruce and moss, which in turn caused leaf N:C ratios to be reduced from set maximum values of 22.5 mg g DM⁻¹ (= 0.05 g N g⁻¹ C from Table 2) to 10.3 mg g DM⁻¹ as described in section 2.1.4. Lower storage and leaf N:C ratios caused specific activities and areal densities of leaf rubisco and chlorophyll to be reduced from the set maximum values given in Table 2.

These activities and densities determined the modeled responses of leaf CO₂ fixation and stomatal conductance to irradiance, temperature and C_a shown in Figure 1. The slope of

the irradiance response curve at low irradiance (Figure 1a) was determined by the quantum and carboxylation efficiencies used to calculate light reaction rates in the model (Table 2). The transition to irradiance-saturated CO₂ fixation at higher irradiance was determined by the specific activities of chlorophyll and rubisco under current storage and leaf N:C, temperature and C_a . Stomatal conductance rose with CO₂ fixation under increasing irradiance (Figure 1b) as required in the model to conserve the C_i/C_a ratio.

The response of CO₂ fixation to rising temperature in the model arose from complex interactions among several processes. These included changing aqueous CO₂ versus O₂ concentrations caused by declining gaseous solubilities, changing carboxylation, oxygenation and electron transport rates caused by more rapid reaction kinetics, and declining turgor potentials, and hence stomatal conductances, caused by increasing vapor pressure differences and hence transpiration rates. These interactions caused simulated leaf CO₂ fixation and stomatal conductance to increase with temperature below 23°C, and to decrease with temperature above 23°C for the conditions of irradiance, C_a and vapor pressure under which the field chamber measurements were taken (Figure 1c and d). Increases at lower temperatures were attributed in the model to more rapid reaction kinetics arising from the Arrhenius function for carboxylation, while declines at higher temperatures were attributed to lower CO₂:O₂ ratios, lower turgor potentials and higher maintenance respiration. These lower potentials were calculated from the convergence solution described above for equilibrating soil-root-canopy water uptake with canopy-atmosphere vapor diffusion under canopy-atmosphere vapor pressure gradients that rose with temperature. Leaf CO₂ fixation rates measured in this study changed little with temperature, although fixation rates measured in other studies of spruce [e.g. Man and Lieffers, 1997] have shown a temperature sensitivity similar to that in the model.

The response of CO₂ fixation to rising C_a in the model was determined by the relationship between aqueous CO₂ concentration and the K_m for carboxylation (Table 2) as affected by the K_m for oxygenation and by temperature. The decline in stomatal conductance with rises in C_a > 50 $\mu\text{mol mol}^{-1}$ were required in the model to conserve the C_i/C_a ratio. The leaf CO₂ fixation rate in the model reached 18.34 $\mu\text{mol m}^{-2} \text{s}^{-1}$ under high irradiance (1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$), temperature (27°C), C_a (10⁴ $\mu\text{mol mol}^{-1}$) and vapor pressure (2.2 kPa). This rate indicated maximum activity of rubisco and chlorophyll in the model under site growth conditions. It compared with rates of 18.93 and

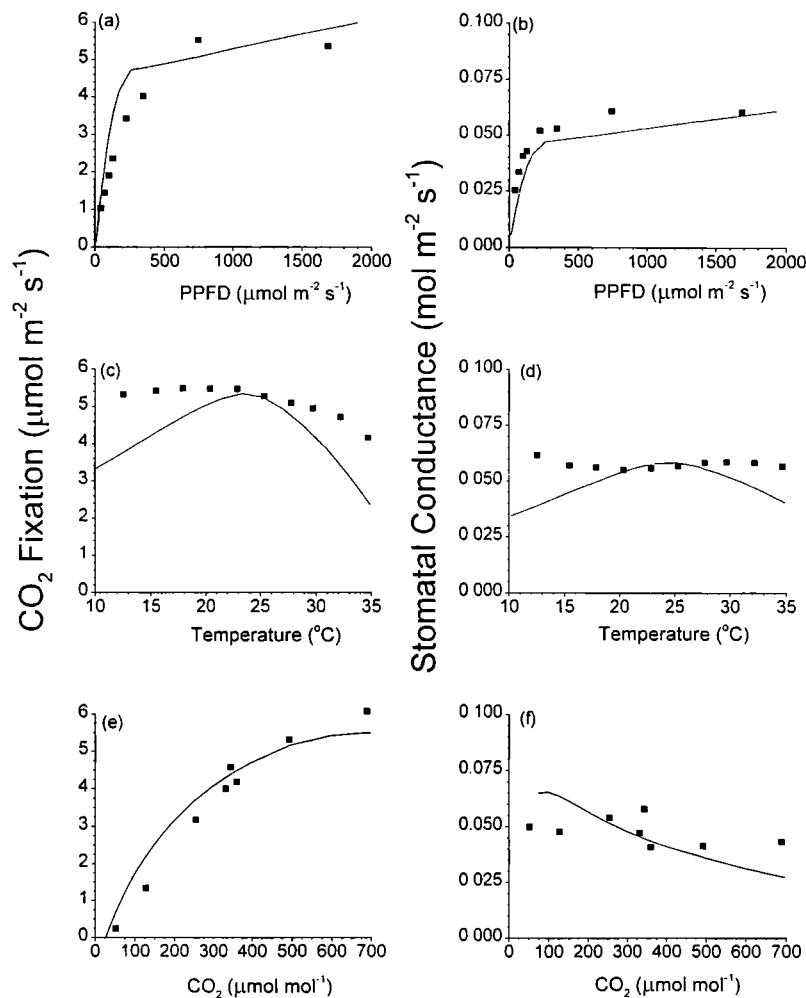


Figure 1. Simulated (lines) and measured (symbols) responses of CO₂ fixation and stomatal conductance by needles in the upper part of a spruce canopy to changes in (a, b) irradiance ($C_a = 355 \mu\text{mol mol}^{-1}$, $T_a = 15^\circ\text{C}$, $H_a = 1.3 \text{ kPa}$), (c, d) air temperature ($C_a = 345 \mu\text{mol mol}^{-1}$, $I = 1800 \mu\text{mol m}^{-2} \text{ s}^{-1}$, H_a increased with temperature from 1.1 to 2.0 kPa), and CO₂ concentration ($I = 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$, $T_a = 11^\circ\text{C}$, $H_a = 1.0 \text{ kPa}$). CO₂ fluxes are expressed per unit hemispherical leaf area.

$16.59 \mu\text{mol m}^{-2} \text{ s}^{-1}$ measured under these same conditions by Middleton *et al.* [1997] on needles harvested from the old black spruce site on July 28 and September 13, 1994, and with rates of $16\text{--}24 \mu\text{mol m}^{-2} \text{ s}^{-1}$ estimated from temperature, irradiance and C_i response functions of CO₂ fixation at this site in July 1996 by Rayment *et al.* [submitted] (M.B. Rayment *et al.*, Photosynthesis and respiration of black spruce at three organizational scales: shoot, branch & canopy, submitted to *Plant Cell Environ.* 1999). Both measured and modeled CO₂ fixation rates and stomatal conductances of spruce were less than half those of aspen reported by Grant *et al.* [1999a].

5.2. Diurnal Mass and Energy Exchange

During the second week of June 1994 the weather recorded at the field site changed from sunny and warm (day of year (DOY) 159–161) to cloudy and cool (DOY 162–165) (Figure 2a) with some precipitation during DOY 164 (Figure 2b). By this time the upper 0.2 m of the soil had thawed, but both measured and modeled soil temperatures remained between 5°C and 15°C in

the upper 0.10 m (Figure 2c) and near 0°C below. In the model, radiation reaching the ground surface was mostly returned to the atmosphere as latent and sensible heat from the moss canopy and from the detritus layer underneath, rather than conducted as heat into the soil, so that soil warming was slow. Changes in weather caused net radiation measured and modeled over the black spruce canopy to change from higher values during the first 3 days of the week to lower values during the next 4 days (Figure 3a). The low albedo of the spruce-moss ecosystem is indicated by midday fluxes of up to 600 W m^{-2} . The canopy conductance by which net radiation is partitioned into latent and sensible heat fluxes in the model is aggregated directly from the leaf-level values demonstrated in Figure 1. Both measured and modeled latent heat fluxes were low ($< 200 \text{ W m}^{-2}$) and stable during the entire week so that changes in net radiation were offset mostly by changes in sensible heat in the model as was reported at the field site [Jarvis *et al.*, 1997; Pattey *et al.* 1997]. Modeled Bowen ratios reached values of 2 or more on sunny, warm days but remained lower on cloudy, cool days. The average midday

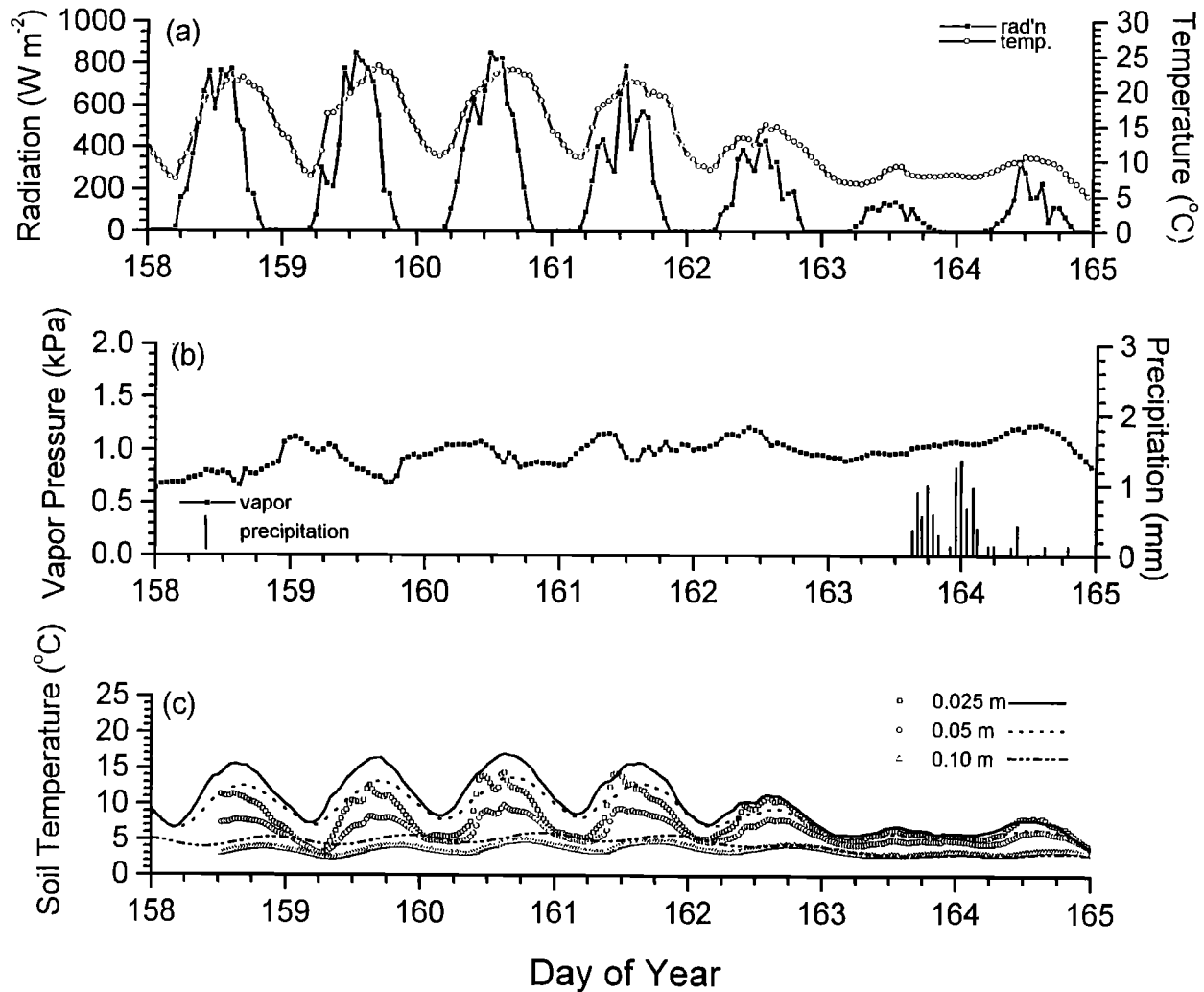


Figure 2. (a) Radiation, air temperature, (b) vapor pressure, precipitation, and (c) soil temperature measured (symbols) and modeled (lines) at depths of 0.025, 0.05, and 0.10 m in the old black spruce site of the BOREAS southern study area from June 8 (DOY 159) to June 14 (DOY 165), 1994.

Bowen ratio measured at the field site during this period was 1.9 [Jarvis *et al.*, 1997]. During this period soil water content in the model remained high (due to ice layers and consequent poor drainage in the mineral soil) so that canopy turgor remained above values at which stomatal conductance was affected by plant water status.

Modeled ecosystem CO_2 fluxes are the sum of all leaf fluxes in black spruce (Figure 1) and moss, minus total autotrophic plus heterotrophic respiration by black spruce, moss and the soil. Net downward fluxes modeled and measured above the spruce canopy during daytime reached $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ under higher radiation and temperature during the second week of June (Figure 3b). These fluxes declined with radiation and temperature to midday rates of $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ under cool, overcast conditions later in the week. Upward fluxes during nights declined from 5 to $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the model and from 3 to $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the field with soil cooling during the same period (Figure 2c). Measured CO_2 fluxes were sometimes lower

during warmer days (e.g. DOY 161) and higher during cooler days (e.g. DOY 163) due to the temperature sensitivity of heterotrophic respiration.

Weather reported from the field site during the last week of July indicated rising temperature and humidity from DOY 205 through 209, followed by a brief rainy period during DOY 209 and 210 (Figure 4a and b). Soil temperatures reached a maximum of 20°C near the surface, but remained $\sim 10^{\circ}\text{C}$ at 0.10 m and cooler below (Figure 4c). Rising humidity caused Bowen ratios in the model and in the field to decline from ~ 2 under drier conditions at the beginning of the week to ~ 1 under more humid conditions later in the week (Figure 5a). The average midday Bowen ratio measured at the field site during this period was 1.3–1.4 [Jarvis *et al.*, 1997]. These Bowen ratios contrast with those of < 0.5 measured by eddy covariance [Blanken *et al.*, 1997] and modeled by *ecosys* [Grant *et al.*, 1999a] during the same period over a nearby aspen stand. During this period soil water content in the model remained above field capacity so that

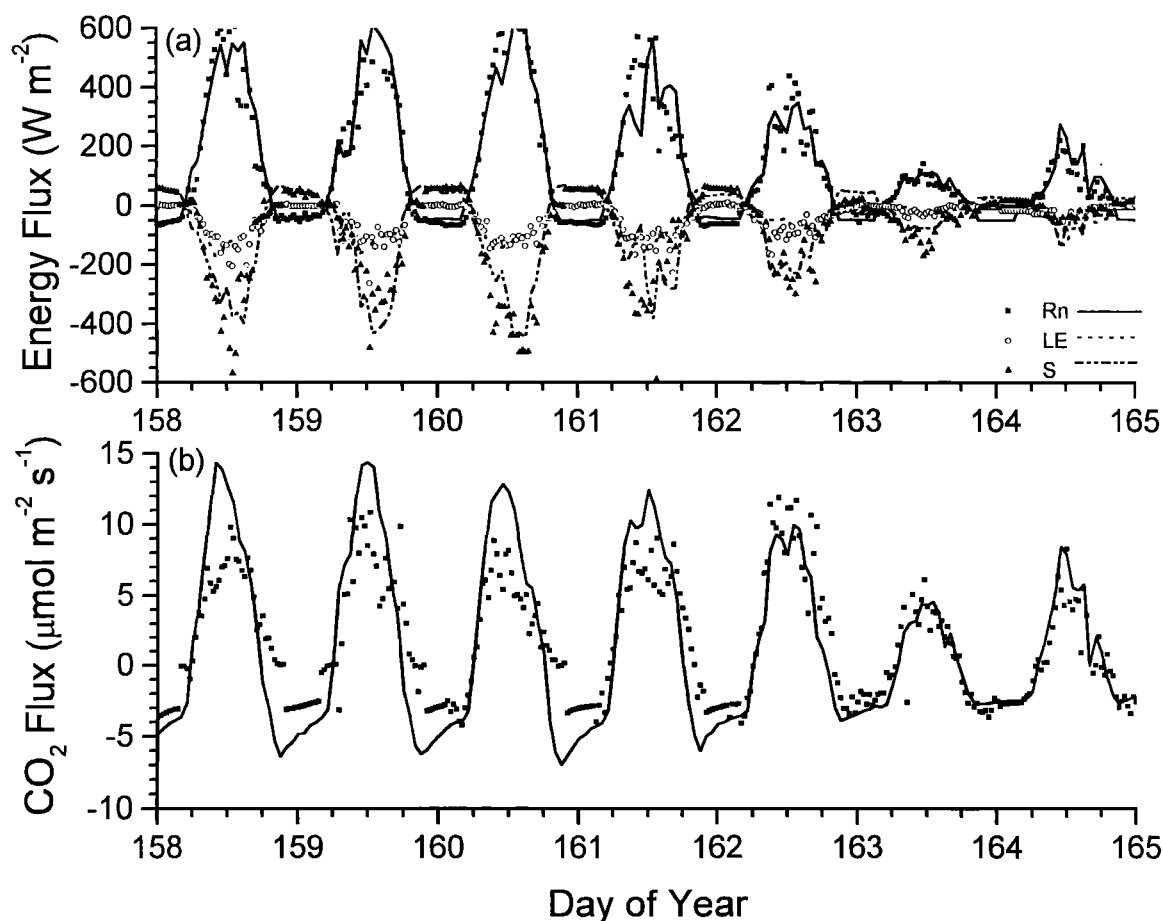


Figure 3. (a) Net radiation (R_n), latent (LE) and sensible (S) heat fluxes and (b) CO_2 fluxes simulated (lines) and measured (symbols) at the southern old black spruce site from June 8 (DOY 159) to June 14 (DOY 165), 1994.

under rising humidity canopy turgor remained above values at which stomatal conductance was affected by plant water status. Modeled latent heat fluxes were sensitive to evaporation of intercepted precipitation from spruce foliage (e.g. afternoon of DOY 209) which was constrained only by boundary layer resistance.

Net downward CO_2 fluxes modeled over the black spruce canopy during daytime in the last week of July (Figure 5b) were less than those during the second week of June (Figure 3b), because autotrophic and heterotrophic respiration became more rapid under higher temperatures (Figure 4a versus Figure 2a). Downward fluxes remained below $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the days while upward fluxes rose from 6 to $9 \mu\text{mol m}^{-2} \text{s}^{-1}$ under rising temperatures during the nights, due mostly to larger soil efflux both in the model and at the field site. These upward fluxes were larger than those during late May because both measured and modeled temperatures in the organic soil zone had reached 15°C – 20°C (Figure 4c), and the mineral soil below had completely thawed by late July.

The contribution of moss to mass and energy exchange in the spruce-moss stand is indicated by the fluxes simulated over the moss layer (Figure 6). Daytime net radiation modeled over this layer was ~ 0.15 of that over the black spruce during the last

week of July (Figure 6a). In the model daytime moss temperatures were higher than those of the air while soil surface temperatures were lower, so that upward sensible heat fluxes from the moss to the air were offset by downward fluxes from the air to the soil. Both the moss and the soil surface contributed upward latent heat fluxes to the atmosphere.

Modeled daytime CO_2 fixation by the moss offset autotrophic plus heterotrophic respiration from the soil and moss so that downward CO_2 fluxes of 1 – $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ were simulated above the moss during most days (Figure 6b). However these fluxes were smaller than those of respiration at night so that the modeled soil-moss system was a net emitter of CO_2 . A similar relationship between CO_2 fixation and respiration over a moss layer in a black spruce-moss forest was measured by Goulden and Crill [1997]. The average modeled rate of daytime CO_2 fixation by moss during this period was $\sim 3 \mu\text{mol m}^{-2} \text{s}^{-1}$ from a phytomass of 40 g C m^{-2} . This rate is equivalent to $3 \text{ mg C g C}^{-1} \text{ h}^{-1}$ which is close to average values of $2 \text{ mg C g C}^{-1} \text{ h}^{-1}$ reported from controlled environment chambers by Busby and Whitfield [1977] and others [e.g. Proctor, 1982].

Radiation fluxes reported from the field site during the second week of September were lower than those during May and July (Figure 7a). The weather changed from warm and clear

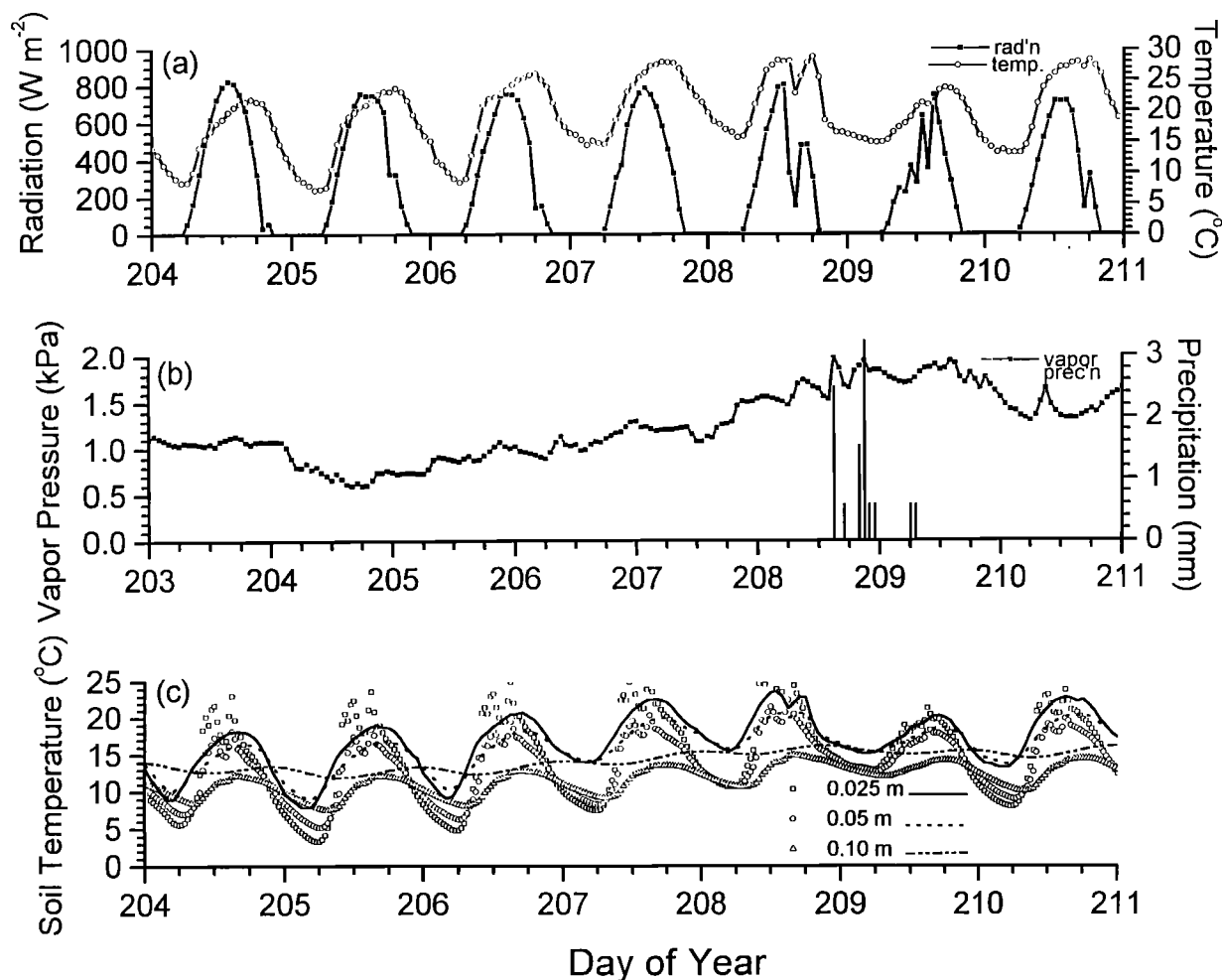


Figure 4. (a) Radiation, air temperature, (b) vapor pressure, precipitation, and (c) soil temperature measured (symbols) and modeled (lines) at depths of 0.025, 0.05, and 0.10 m in the old black spruce site of the BOREAS southern study area from July 24 (DOY 205) to July 30 (DOY 211), 1994.

between DOY 250 and 252 to cool and overcast on DOY 253 and 254 and then warmed again during DOY 255 and 256. Soil temperatures near the surface declined during the week to $< 5^{\circ}\text{C}$ but remained warmer below (Figure 7c). Net radiation modeled above the spruce canopy remained below 500 W m^{-2} because of solar angles. Latent heat fluxes in the model rarely exceeded 150 W m^{-2} , so that midday Bowen ratios sometimes exceeded 2 (Figure 8a). Average midday Bowen ratios measured during this period were 1.3–1.4 [Jarvis *et al.*, 1997]. Soil water content remained above field capacity in the model following rainfall on DOY 247, so that canopy turgor remained above values at which stomatal conductance was affected by plant water status.

Daytime CO_2 fluxes modeled and measured during the second week of September were between 5 and $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Figure 8b) which was similar to those during July (Figure 5b). The tendency in the model to underestimate leaf CO_2 fixation at lower temperatures (Figure 1c) did not cause the model to underestimate canopy CO_2 fixation during cooler weather. Nighttime fluxes in the model and the field declined from 5 to $3 \mu\text{mol m}^{-2} \text{ s}^{-1}$ as weather cooled during the week. These rates

were less than those during late July because both measured and modeled temperatures in the organic soil zone had declined to 10°C – 15°C by early September (Figure 7c).

5.3. Annual C Exchange

By summing CO_2 fluxes recorded continuously between May 23 and September 21, 1994 (e.g. Figures 3b, 5b and 8b), Jarvis *et al.* [1997] estimated that the forest ecosystem at the southern old black spruce site was a net sink of 95 g C m^{-2} during these four months. In the model the sum of net CO_2 fluxes by spruce (199 g C m^{-2}), moss (75 g C m^{-2}) and soil/detritus (-218 g C m^{-2}) was 56 g C m^{-2} during this same period. Similarly Jarvis *et al.* [1997] estimated total evapotranspiration between May 23 and September 21, 1994 to be 237 mm by summing continuous measurements of latent heat flux (e.g. Figures 3a, 5a and 8a). In the model the sum of evapotranspiration by spruce, moss and the soil/detritus surfaces was 252 mm during this same period.

The annual C balances of the spruce/moss forest simulated by *ecosys* with 1994 climate data and estimated from flux measurements and allometric techniques during 1994 are given

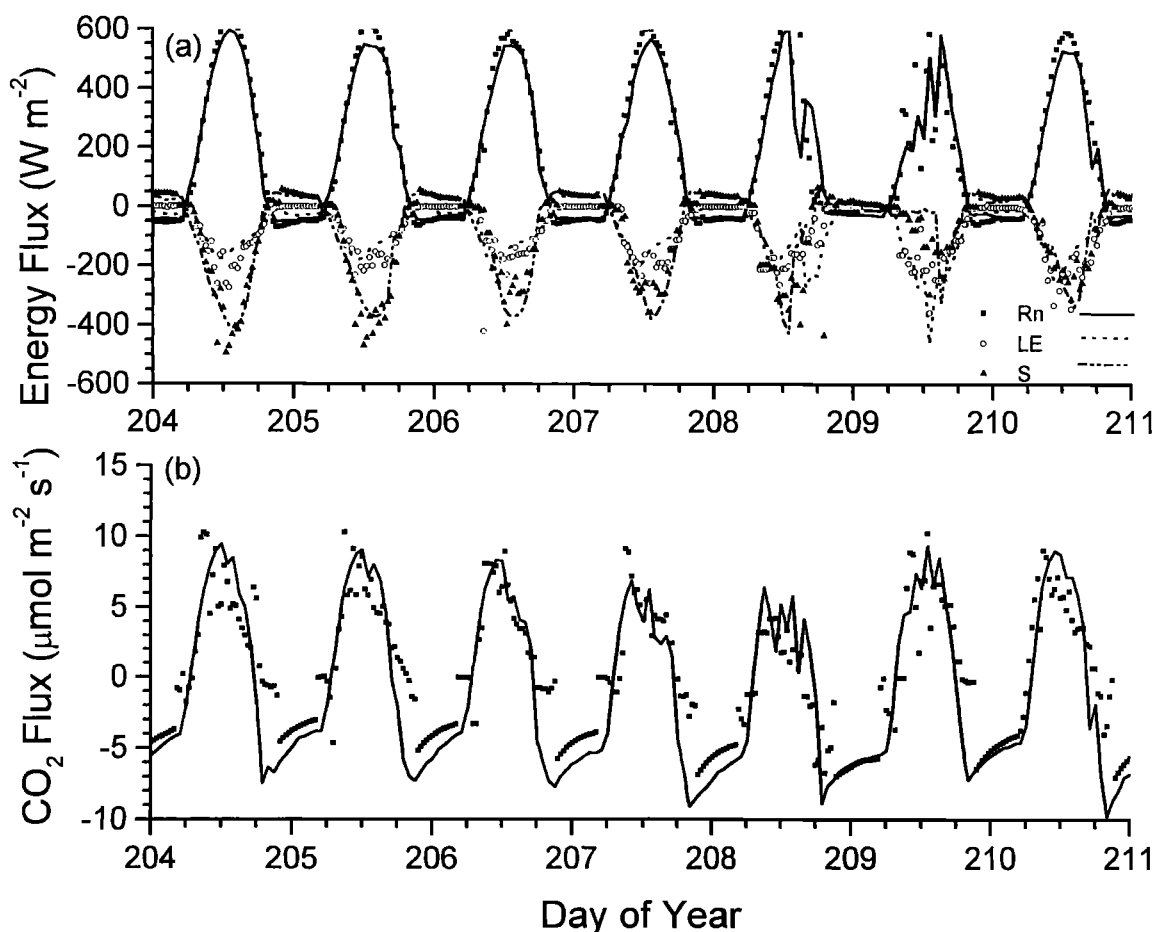


Figure 5. (a) Net radiation (R_n), latent (LE) and sensible (S) heat fluxes and (b) CO_2 fluxes simulated (lines) and measured (symbols) at the southern old black spruce site from July 24 (DOY 205) to July 30 (DOY 211), 1994.

in Table 4. The ratio of autotrophic respiration to gross CO_2 fixation of spruce in the model ($429/660 = 0.65$) was larger than that of aspen in Grant *et al.* [1999a] ($380/811 = 0.47$) even though the same growth and maintenance respiration coefficients were used (Table 2). This increase occurred because the modeled coniferous growth habit caused larger and more persistent accumulations of leaf C and N than did the deciduous. The black spruce NPP of 231 g C m^{-2} was mostly returned to the soil through senescence or exudation. The combined measurements of Gower *et al.* [1997] and Steele *et al.* [1997] indicated an NPP (excluding moss) of 266 g C m^{-2} by trees (almost entirely spruce) at the southern old black spruce site. The gross fixation of 288 g C m^{-2} by moss in the model was 0.30 of that by the spruce/moss ecosystem. Goulden and Crill [1997] reported that moss accounted for 0.10–0.50 of total C fixation at the black spruce/sphagnum moss site in the northern study area of BOREAS. In the model the annual moss NPP of 104 g C m^{-2} was returned to the soil through senescence or exudation. This return fall within the range of 50 to $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ estimated by Harden *et al.* [1997] for C inputs under upland sphagnum, although these estimates may have included some spruce litter. Annual soil respiration in the model, including heterotrophic respiration by microbial communities (294 g C m^{-2}), and

autotrophic respiration by roots and above-ground moss (196 g C m^{-2}), was 490 g C m^{-2} . This was larger than the total soil plus root respiration of 368 and 283 g C m^{-2} estimated from chamber flux measurements on well and poorly drained soils between May 1994 and May 1995 at this site by Nakane *et al.* [1997].

Annual rates of gross fixation and autotrophic respiration under 1994 climate were 948 and 613 g C m^{-2} in the model, ~ 0.2 less than rates of 1090 and 785 g C m^{-2} estimated by Ryan *et al.* [1997] from chamber flux measurements. The resulting NPP of 335 g C m^{-2} is comparable with those estimated from field measurements [e.g. Gower *et al.*, 1997; Ryan *et al.*, 1997] but includes a comparatively large moss component. Annual NEE in the model was thus 41 g C m^{-2} which was the difference between a net gain of 83 g C m^{-2} by the spruce and a net loss of 42 g C m^{-2} by the soil.

5.4. Long-Term C Accumulation

Annual heterotrophic respiration in the model (e.g. Table 4) was influenced by antecedent C storage in the spruce, moss and forest floor which in turn was affected by antecedent climate through its effects on C fixation, respiration and litterfall. For example a heavy litterfall the previous autumn would generate more rapid heterotrophic respiration the following year, causing

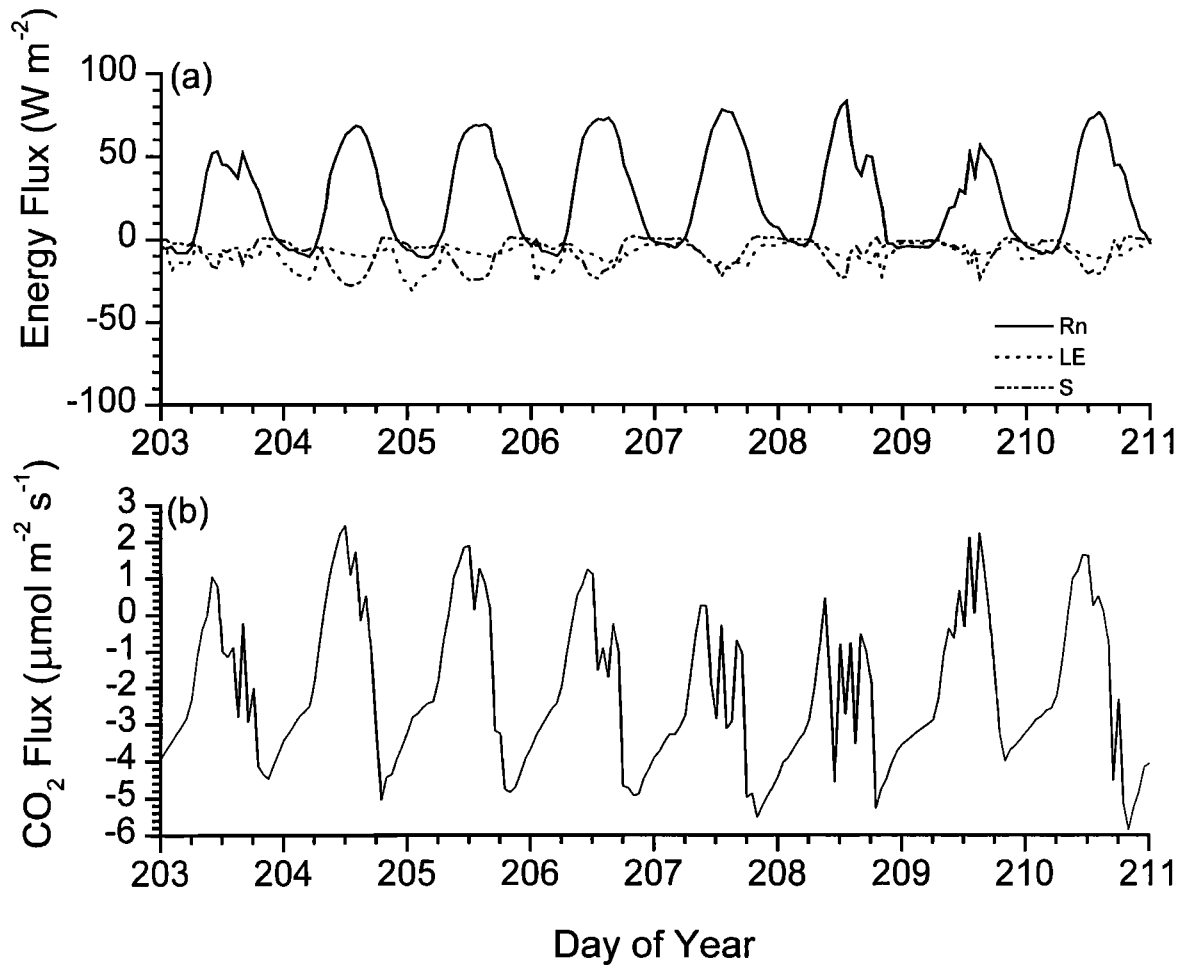


Figure 6. (a) Net radiation (R_n), latent (LE) and sensible (S) heat fluxes and (b) CO_2 fluxes simulated over the moss layer at the southern old black spruce site from July 24 (DOY 205) to July 30 (DOY 211), 1994.

an unrepresentative loss of soil C. More definitive estimates of annual NEP in this forest should therefore be derived from values simulated over several years. When run over 150 years under current atmospheric conditions, the model indicated very slow wood C accumulation during the first 75 years after planting because N and P were sequestered by C turnover in moss (Figure 9a). After 75 years the spruce fully shaded the moss, reducing its C turnover and releasing some of its N and P for spruce growth. Spruce wood C then accumulated at a stable rate of $60 \text{ g C m}^{-2} \text{ yr}^{-1}$. Total C accumulation modeled in wood, foliage and living moss after 115 years (3725 , 380 and 40 g C m^{-2}) was slightly less than that measured by Gower *et al.* [1997] (4300 , 500 and 60 g C m^{-2}), but rising. Under IS92a climate change (Table 3), spruce wood C accumulated in the model at a rate of $90 \text{ g C m}^{-2} \text{ yr}^{-1}$ between 75 and 125 years, but slowed thereafter because of growing N deficits (Figure 9a). This rate rose to $> 150 \text{ g C m}^{-2} \text{ yr}^{-1}$ when NH_4^+ and NO_3^- concentrations in precipitation were raised from 0.25 to 1.0 g m^{-3} . Wood C accumulation derived from allometric equations for growth of black spruce at sites with fair, medium and good productivity indices [Alberta Forest Service, 1985] are provided for comparison with modeled values.

Soil C declined during the first 50 years of the model run under current atmospheric conditions, and then accumulated at an average rate of $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Figure 9b). Nakane *et al.* [1997] estimated soil C accumulations of $3\text{--}13 \text{ g C m}^{-2}$ 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 $10\text{--}30 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the northern old black spruce site. Higher soil temperatures and hence heterotrophic respiration under IS92a climate change caused soil C loss to continue until year 100, and delayed soil C accumulation until after year 125 (Figure 9b). The additional losses of soil C under IS92a were largely eliminated by the increase of mineral N concentration in precipitation.

6. Discussion

Mass and energy exchanges over black spruce forests are characterized by low CO_2 fixation rates and high Bowen ratios (Figures 3, 5 and 8) even though these exchanges are not limited by soil water. Modeled CO_2 fixation in black spruce was strongly constrained by low N:C ratios in leaf storage pools that reduced

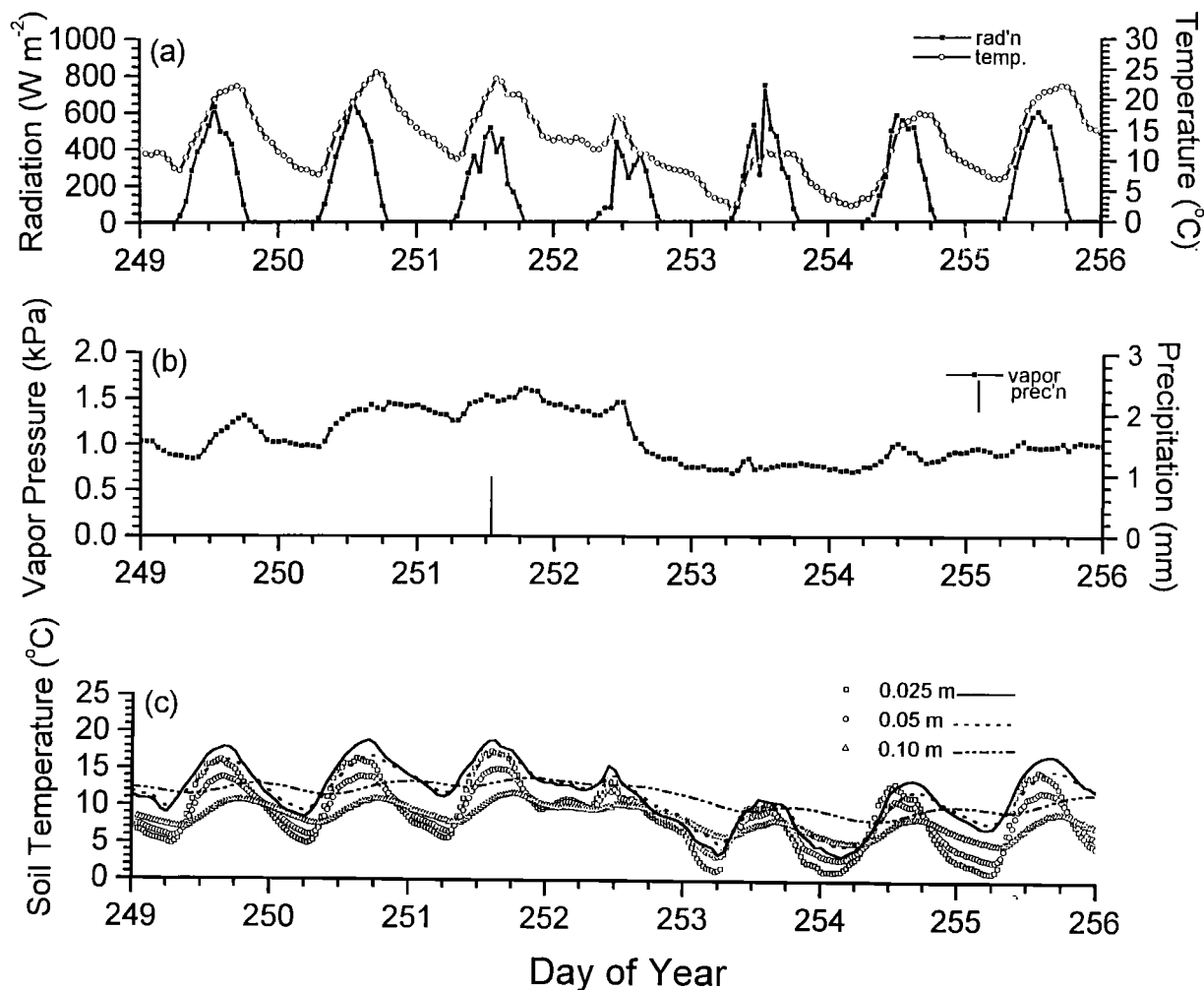


Figure 7. (a) Radiation, air temperature, (b) vapor pressure, precipitation, and (c) soil temperature measured (symbols) and modeled (lines) at depths of 0.025, 0.05, and 0.10 m in the old black spruce site of the BOREAS southern study area from September 7 (DOY 250) to September 13 (DOY 256), 1994.

the specific activities (Figure 1) and surface densities of leaf chlorophyll and rubisco to less than half of maximum values set from fertilization experiments (Table 2). These low N:C ratios occurred in the model because plant N uptake was limited by extremely low NH_4^+ and NO_3^- 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 2), and from the slow mineralization of soil organic matter caused by its high soil C:N ratios (Table 1). 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 ($\sim 500 \text{ g C m}^{-2}$ in the model which was also measured at most black spruce sites sampled by Halliwell *et al.*, 1995] that accumulated under the spruce and the moss. Reduced microbial activity was apparent in the lower annual rate of heterotrophic respiration modeled at the southern old black spruce site (294 g C m^{-2} in Table 4) versus that at the nearby southern old aspen site (525 g C m^{-2} by Grant *et al.*, 1999a).

This lower rate is consistent with the lower estimate of annual soil respiration at the spruce site by Nakane *et al.* [1997] versus that at the aspen site by Black *et al.* [1996]. Low microbial activity in the model under spruce also resulted in low rates of N_2 fixation ($\sim 0.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ under spruce versus $2.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ under aspen in Grant *et al.*, 1999a] that also contributed to low soil NH_4^+ and NO_3^- concentrations. These fixation rates are within the ranges of $0.03\text{--}1.85 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $0.35\text{--}3.25 \text{ g N m}^{-2} \text{ yr}^{-1}$ 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, the rooting depth of which was confined to the low pH zone).

Low CO_2 fixation rates caused by low N:C ratios forced low stomatal conductances in the model (Figure 1), based on the assumed conservation of the C_i/C_a ratio. Low conductances in spruce (typically $0.02\text{--}0.04 \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under full sunlight) were inferred from leaf chamber and C isotope discrimination studies by Flanagan *et al.* [1997] and measured with a portable

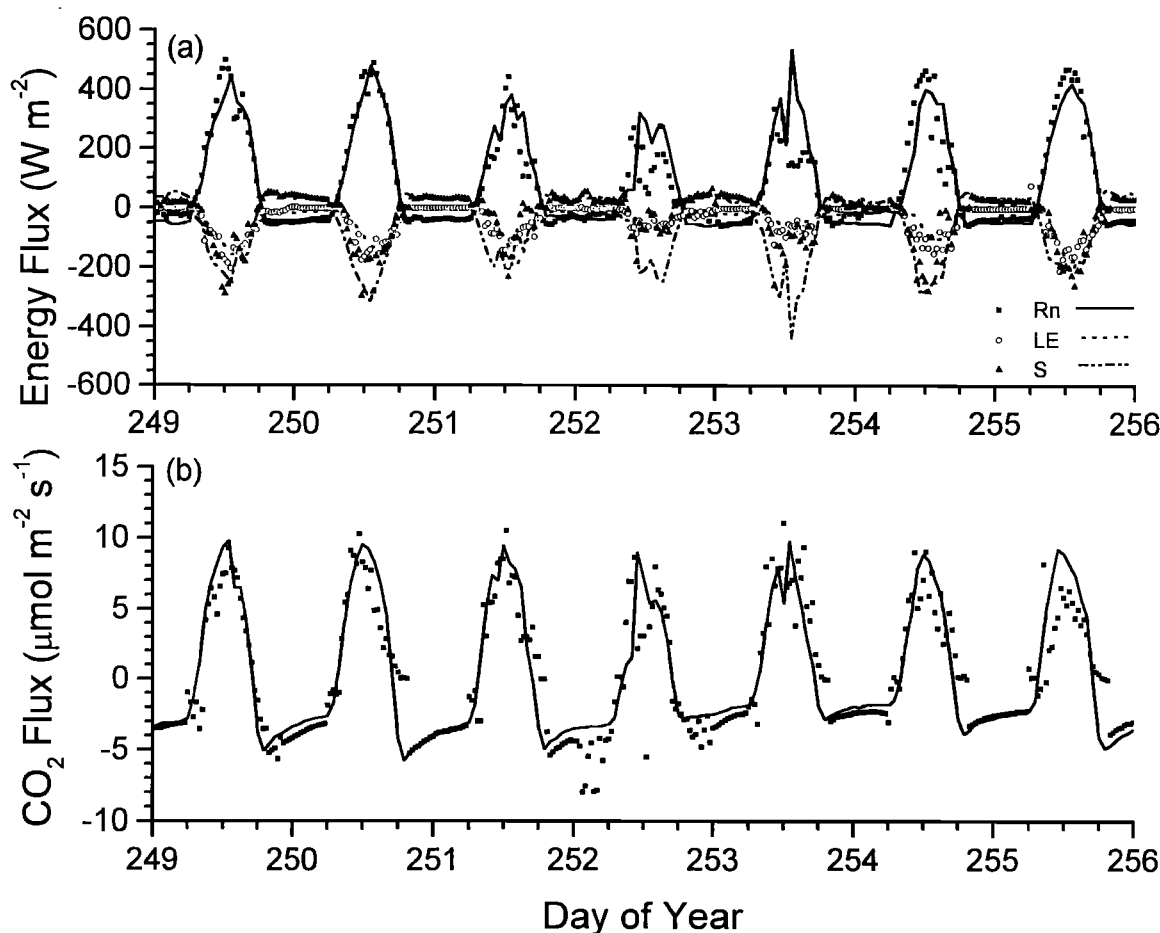


Figure 8. (a) Net radiation (R_n), latent (LE) and sensible (S) heat fluxes and (b) CO_2 fluxes simulated (lines) and measured (symbols) at the southern old black spruce site from September 7 (DOY 250) to September 13 (DOY 256), 1994.

photosynthesis system by Middleton *et al.* [1997]. These low conductances caused the small latent heat fluxes and large sensible heat fluxes modeled in Figures 3a, 5a and 8a. Because the response of CO_2 fixation (Figure 1a) and stomatal conductance (Figure 1b) to irradiance above $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ was limited, increases in net radiation were mostly offset by increases in sensible heat flux, as has 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 ($\sim 100 \text{ mm yr}^{-1}$). 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 O_2 concentrations occasionally reduced microbial activity [Grant and Pattey, 1999] (Table 2). Low soil temperatures and O_2 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 [Liefjers 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 detritus \rightarrow slow detritus decomposition \rightarrow slow nutrient mineralization \rightarrow surface detritus accumulation \rightarrow cold soil \rightarrow slow nutrient uptake \rightarrow low CO_2 fixation \rightarrow low transpiration \rightarrow wet soil \rightarrow slow detritus decomposition \rightarrow slow nutrient mineralization ...) that caused NPP and NEP to stabilize at low values (Table 4; Figure 9). Evidence from the model supports the hypothesis that soil N availability is an important constraint to mass and energy exchange over black spruce.

Rates of mass and energy exchange simulated by *ecosys* at the southern old black spruce site (Figures 3, 5 8; Table 4) were lower than those at the southern old aspen site [Grant *et al.*, 1999a, Figures 4, 5, 7, 8, 10, 11 and Table 4] where simulated microbial activity was more rapid. Nonetheless the modeled spruce/moss forest remained a stable net sink for atmospheric C of about $60 \text{ (wood)} + 10 \text{ (soil)} = 70 \text{ g C m}^{-2} \text{ yr}^{-1}$ (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 O_2 contents of the soil. Nakane *et al.* [1997] used measurements and models of litterfall and soil respiration to estimate net gains in soil C at this site

Table 4. Annual Carbon Balance of a Black Spruce - Moss Forest Simulated by *Ecosys* With 1994 Climate, and Estimated From Flux Measurements and Allometric Techniques During 1994

	Simulated, g C m ⁻²	Estimated, g C m ⁻²
<i>Spruce</i>		
Gross fixation	660	
Respiration ^a	429	
Net primary productivity	231	
Senescence	128	53 ^d + 120 ^a 91,54 ^e
Exudation	20	
Net growth Wood	64	80 ^d
Foliage	16	8 ^d
Roots	3	
Change in storage	0	
<i>Moss</i>		
Gross fixation	288	
Respiration ^a	184	
Net primary productivity	104	
Senescence	103	37 ^e , 50-150 ^h
Exudation	1	
Net growth	0	12 ^d
Change in storage	0	
<i>Soil</i>		
Respiration ^{b,c}	294	368,283 ^e
<i>Ecosystem</i>		
Gross fixation	948	1090 ^f
Total respiration Autotrophic	613	785 ^f
Heterotrophic	294	
Net primary productivity	335	266 ^{d,g} ,307 ^f
Net ecosystem productivity	41	
Change in plant C	83	
Change in soil C	-42	

^a Includes root respiration.^b Excludes root respiration.^c Includes CO₂-C and CH₄-C.^d Gower *et al.* [1997] Litterfall above-ground only.^e Nakane *et al.* [1997] Well and poorly drained sites. Litterfall above-ground only. Soil respiration includes root respiration.^f Ryan *et al.* [1997].^g Steele *et al.* [1997] From below-ground NPP.^h Harden *et al.* [1997].

during 1994 of 3-13 g m⁻², depending upon subsurface drainage. Harden *et al.* [1997] used ¹⁴C studies to estimate long-term accumulation rates of soil C at the BOREAS northern old black spruce site of 10-30 g C m⁻² yr⁻¹, again depending upon subsurface drainage. The above-ground measurements of ecosystem C at the southern old black spruce site by Gower *et al.* [1997] suggest a long term average wood growth rate of 40-50 g C m⁻² yr⁻¹, which is consistent with that estimated by the *Alberta Forest Service* [1985] at fair to medium sites under comparable climates (Figure 9). These measured and modeled rates of soil and wood C accumulation suggest a net ecosystem productivity of 50-80 g C m⁻² yr⁻¹ by the black spruce/moss forest at this low productivity site in the southern study area of BOREAS. This

rate is less than that one of 100-150 C m⁻² yr⁻¹ simulated [Grant *et al.*, 1999a] and measured [Black *et al.*, 1996] at the southern old aspen site ~ 60 km away where rates of C cycling were larger. However if applied to the entire boreal forest zone, the NEP estimated at the old black spruce site would account for a global sink of 1 Gt C yr⁻¹ [Sellers *et al.*, 1997]. This sink would likely rise under IS92a climate change, but the rise would be partially offset by losses of soil C from more rapid heterotrophic respiration in warming soils. This sink would rise further if rates of atmospheric N deposition were to increase, thereby alleviating N limitations and allowing a stronger response of NPP to elevated C_a as proposed by McGuire *et al.* [1995].

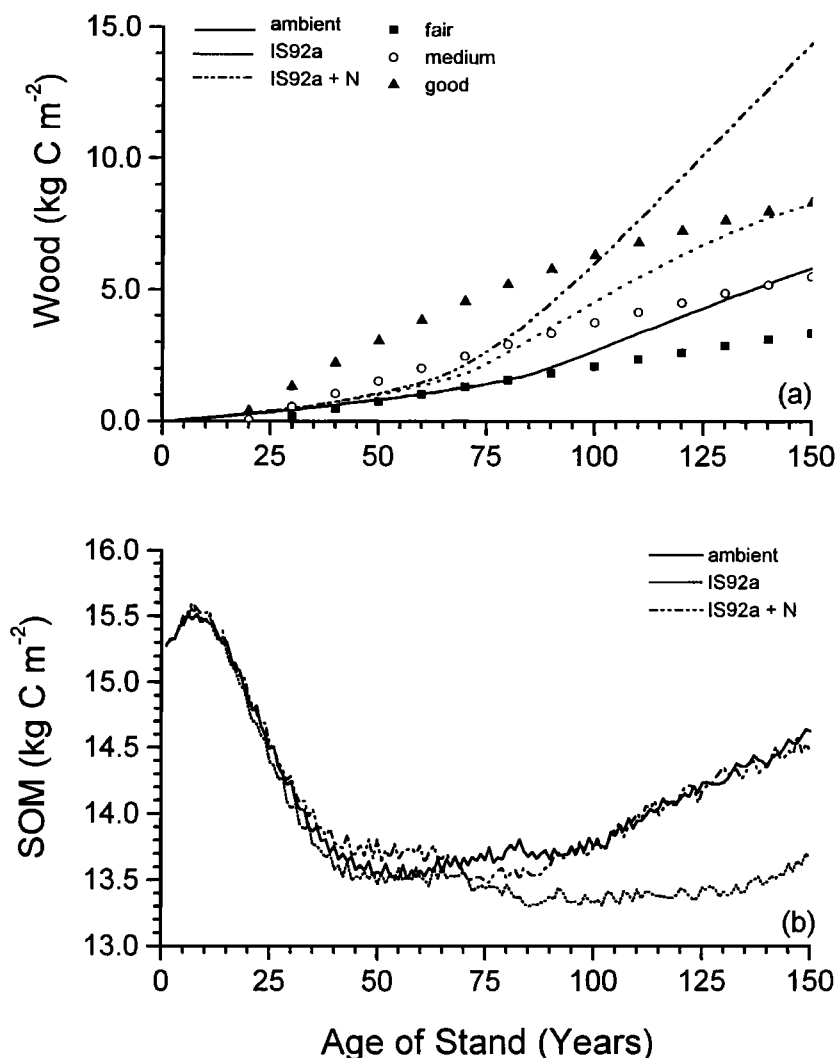


Figure 9. (a) Spruce wood C and (b) soil organic C simulated in a black spruce-moss stand in the southern study area during 150 years under current (1994 - 1996) climate (lines), and spruce wood C at fair and medium sites calculated from wood volume measurements by the *Alberta Forest Service* [1985] (symbols).

References

- Alberta Forest Service, *Alberta Phase 3 Forest Inventory: Yield Tables for Unmanaged Stands*, Alberta Energy and Natl. Resour., Edmonton, Alberta, 1985.
- Betts, A.K., and J.H. Ball, Albedo over the boreal forest, *J. Geophys. Res.*, **102**, 28,901-28,909, 1997.
- Black, T.A., et al., Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest, *Global Change Biol.*, **2**, 219-229, 1996.
- Blanken, P.D., T.A. Black, P.C. Yang, H.H. Neumann, Z. Nesic, R. Staebler, G. den Hartog, M.D. Novak, and X. Lee, Energy balance and canopy conductance of a boreal aspen forest: Partitioning overstory and understory components, *J. Geophys. Res.*, **102**, 28,915-28,927, 1997.
- Brouzes, R., J. Lasik, and R. Knowles, The effect of organic amendment, water content and oxygen on the incorporation of ¹⁵N₂ by some agricultural and forest soils, *Can. J. Microbiol.*, **15**, 899-905, 1969.
- Busby, J.R., and D.W.A. Whitfield, Water potential, water content, and net assimilation of some boreal forest mosses, *Can. J. Bot.*, **56**, 1551-1558, 1977.
- Campbell, T.A., Oxygen flux measurements in organic soils, *Can. J. Soil Sci.*, **60**, 641-650, 1980.
- Chen, J.M., P.M. Rich, S.T. Gower, J.M. Norman, and S. Plummer, Leaf area index of boreal forests: Theory, techniques and measurements, *J. Geophys. Res.*, **102**, 29,429-29,443, 1997.
- Ciais, P., P.P. Tans, J.W.C. White, M. Trolier, R.J. Francey, J.A. Berry, D.R. Randall, P.J. Sellers, J.G. Collatz, and D.S. Schimel, Partitioning of ocean and land uptake of CO₂ as inferred by $\delta^{13}\text{C}$ measurements from the NOAA Climate Monitoring and Diagnostic Laboratory Global Air Sampling Network, *J. Geophys. Res.*, **100**, 5051-5070, 1995.
- Clymo, R.S., and P.M. Hayward, The ecology of *Sphagnum*, in *Bryophyte Ecology*, edited by A.J.E. Smith, pp. 229-289, Chapman and Hall, 1982.
- Farquhar, G.D., S. von Caemmerer and J.A. Berry, A

- biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species, *Planta*, 149, 78-90, 1980.
- Flanagan, L.B., J.R. Brooks, and J.R. Ehleringer, Photosynthesis and carbon isotope discrimination in boreal forest ecosystems: A comparison of functional characteristics in plants from three mature forest types, *J. Geophys. Res.*, 102, 28,861-28,869, 1997.
- Goulden, M.L., and P.M. Crill, Automated measurements of CO₂ exchange at the moss surface of a black spruce forest, *Tree Physiol.*, 17, 537-542, 1997.
- Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, S.J. Steele and T.K. Stow, Carbon distribution and aboveground net primary production in aspen, jack pine and black spruce stands in Saskatchewan and Manitoba, Canada, *J. Geophys. Res.*, 102, 29,029-29,041, 1997.
- Grant, R.F., The distribution of water and nitrogen in the soil-crop system: A simulation study with validation from a winter wheat field trial, *Fert. Res.*, 27, 199-214, 1991.
- Grant, R.F., Simulation model of soil compaction and root growth, I, Model development, *Plant Soil*, 150, 1-14, 1993a.
- Grant, R.F., Simulation model of soil compaction and root growth, II, Model testing, *Plant Soil* 150, 15-24, 1993b.
- Grant, R.F., Simulation of competition between barley (*Hordeum vulgare* L.) and wild oat (*Avena fatua* L.) under different managements and climates, *Ecol. Model.*, 71, 269-287, 1994a.
- Grant, R.F. Simulation of ecological controls on nitrification, *Soil Biol. Biochem.* 26, 305-315, 1994b.
- Grant, R.F., Mathematical modelling of nitrous oxide evolution during nitrification, *Soil Biol. Biochem.* 27, 1117-1125, 1995.
- Grant, R.F., *Ecosys.* in *Global Change and Terrestrial Ecosystems Focus 3 Wheat Network: Model and Experimental Meta. Data*, 2nd Ed., pp. 65-74, GCTE Focus 3 Office, NERC Centre for Ecol. and Hydrol., Wallingford, Oxon, U.K., 1996a.
- Grant, R.F., *Ecosys.* in *Global Change and Terrestrial Ecosystems Task 3.3.1 Soil Organic Matter Network (SOMNET): 1996 Model and Experimental Metadata*, pp. 19-24, GCTE Focus 3 Office, NERC Centre for Ecol. and Hydrol., Wallingford, Oxon, U.K., 1996b.
- Grant, R.F., Changes in soil organic matter under different tillage and rotation: Mathematical modelling in *ecosys*, *Soil Sci. Soc. Am. J.*, 61, 1159-1174, 1997.
- Grant, R.F., Simulation of methanogenesis in the mathematical model *ecosys*, *Soil Biol. Biochem.* 30, 883-896, 1998a.
- Grant, R.F., Simulation in *ecosys* of root growth response to contrasting soil water and nitrogen, *Ecol. Model.*, 107, 237-264, 1998b.
- Grant, R.F., Simulation of methanotrophy in the mathematical model *ecosys*, *Soil Biol. Biochem.*, 31, 287-297, 1999.
- Grant, R.F., and D.D. Baldocchi, Energy transfer over crop canopies: simulation and experimental verification, *Agric. For. Meteorol.*, 61, 129-149, 1992.
- Grant, R.F., and D.J. Heaney, Inorganic phosphorus transformation and transport in soils: mathematical modelling in *ecosys*, *Soil Sci. Soc. Am. J.*, 61, 752-764, 1997.
- Grant, R.F., and J.D. Hesketh, Canopy structure of maize (*Zea mays* L.) at different populations: Simulation and experimental verification, *Biotronics*, 21, 11-24, 1992.
- Grant, R.F., and E. Pattey, Mathematical modelling of nitrous oxide emissions from an agricultural field during spring thaw, *Global Biogeochem. Cycles*, 13, 679-694, 1999.
- Grant, R.F., and J.A. Robertson, Phosphorus uptake by root systems: mathematical modelling in *ecosys*, *Plant Soil*, 188, 279-297, 1997.
- Grant, R.F., and P. Rochette, Soil microbial respiration at different temperatures and water potentials: Theory and mathematical modelling, *Soil Sci. Soc. Am. J.*, 58, 1681-1690, 1994.
- Grant, R.F., N.G. Juma, and W.B. McGill, Simulation of carbon and nitrogen transformations in soils. I. Mineralization, *Soil Biol. Biochem.*, 27, 1317-1329, 1993a.
- Grant, R.F., N.G. Juma, and W.B. McGill, Simulation of carbon and nitrogen transformations in soils. II. Microbial biomass and metabolic products, *Soil Biol. Biochem.*, 27, 1331-1338, 1993b.
- Grant, R.F., M. Nyborg, and J. Laidlaw, Evolution of nitrous oxide from soil: I. Model development, *Soil Sci.*, 156, 259-265, 1993c.
- Grant, R.F., M. Nyborg, and J. Laidlaw, Evolution of nitrous oxide from soil: II. Experimental results and model testing, *Soil Sci.*, 156, 266-277, 1993d.
- Grant, R.F., P. Rochette, and R.L. Desjardins, Energy exchange and water use efficiency of crops in the field: Validation of a simulation model, *Agron. J.*, 85, 916-928, 1993e.
- Grant, R.F., R.C. Izaurralde, and D.S. Chanasyk, Soil temperature under different surface managements: Testing a simulation model, *Agric. For. Meteorol.* 73, 89-113, 1995a.
- Grant, R.F., B.A. Kimball, P.J. Pinter Jr., G.W. Wall, R.L. Garcia, and R.L. LaMorte, CO₂ effects on crop energy balance: Testing *ecosys* with a Free-Air CO₂ Enrichment (FACE) Experiment, *Agron. J.*, 87, 446-457, 1995b.
- Grant, R.F., R.C. Izaurralde, M. Nyborg, S.S. Malhi, E.D. Solberg and D. Jans-Hamunernmeister, Modelling tillage and surface detritus effects on soil C storage under current vs. elevated CO₂ and temperature in *ecosys*, in *Soil Processes and the Carbon Cycle*, edited by R. Lal et al., pp. 527-547, CRC Press, Boca Raton, Fla., 1998.
- Grant, R.F., T.A. Black, G. den Hartog, J.A. Berry, H.H. Neumann, P.D. Blanken, P.C. Yang, C. Russell, and I.A. Nalder, Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: testing the mathematical model *ecosys* with data from the BOREAS experiment, *J. Geophys. Res.*, 104, 27,699-27,717, 1999a.
- Grant, R.F., G.W. Wall, K.F.A. Frumau, P.J. Pinter Jr., D. Hunsaker, B.A. Kimball, and R.L. LaMorte, Crop Water Relations under Different CO₂ and Irrigation: Testing of *ecosys* with the Free Air CO₂ Enrichment (FACE) Experiment, *Agric. For. Meteorol.*, 95, 27-51, 1999b.
- Halliwell, D.H., M.J. Apps, and D.T. Price, A survey of the forest site characteristics in a transect through the central Canadian boreal forest, *Water Soil Air Poll.*, 82, 257-270, 1995.
- Harden, J.W., K.P. O'Neill, S.E. Trumbore, H. Veldhuis, and B.J. Stocks, Moss and soil contributions to the annual net carbon flux of a maturing boreal forest, *J. Geophys. Res.*, 102, 28,805-28,816, 1997.
- Itoh, S., and S.A. Barber, Phosphorus uptake by six plant species as related to root hairs, *Agron. J.*, 75, 457-461, 1983.
- Jarvis, P.G., J.M. Massheder, S.E. Hale, J.B. Moncrieff, M.

- Rayment, and S.L. Scott, Seasonal variation in carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest, *J. Geophys. Res.*, 102, 28,953-28,966, 1997.
- Kattenberg, A., F. Giorgi, H. Grassl, G.A. Meehl, J.F.B. Mitchell, R.J. Stouffer, T. Tokioka, A.J. Weaver, and T.M.L. Wigley, Climate models - Projection of future climate, in *Climate Change 1995*, edited by J.T. Houghton et al., pp. 285-357, Cambridge Univ. Press, New York, 1996.
- Keeling, C.D., T.P. Whorff, M. Wahlen, and J. van der Plicht, Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980, *Nature*, 375, 666-670, 1995.
- Lieffers, V.J. and S.E. Macdonald, Growth and nutrient status of black spruce and tamarack in relation to depth of water table in some Alberta peatlands, *Can. J. For. Res.*, 20, 805-809, 1990.
- Lieffers, V.J. and R.L. Rothwell, Rooting of peatland black spruce and tamarack in relation to depth of water table, *Can. J. Bot.*, 65, 817-821, 1987.
- Mahendrappa, M.K. and P.O. Saloni, Nutrient dynamics and growth responses in a fertilized black spruce stand, *Soil Sci. Soc. Am. J.*, 46, 127-133, 1982.
- Man, R. and V.J. Lieffers, Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open, *Tree Physiol.*, 17, 437-444, 1997.
- Middleton, E.M., J.H. Sullivan, B.D. Bovard, A.J. Deluca, S.S. Chan and T.A. Cannon, Seasonal variability in foliar characteristics and physiology for boreal forest species at the five Saskatchewan tower sites during the 1994 Boreal Ecosystem-Atmosphere Study, *J. Geophys. Res.*, 102, 28,831-28,844, 1997.
- McGuire, A.D., J.M. Melillo, and L.A. Joyce, The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon dioxide, *Ann. Rev. Ecol. Syst.*, 26, 473-503, 1995.
- Moncrieff, J.B., J.M. Massheder, A. Verhoef, J. Elbers, B.H. Heutsunkveld, S. Scott, H. de Bruin, P. Kabat, H. Soegaard, and P.G. Jarvis, A system to measure surface fluxes of energy, momentum and carbon dioxide, *J. Hydrol.*, 188-189, 589-611, 1997.
- Mugasha, A.G., D.J. Pluth, K.O. Higginbotham, and S.K. Takyi, Foliar responses of black spruce to thinning and fertilization on a drained shallow peat, *Can. J. For. Res.*, 21, 152-163, 1991.
- Nakane, K., T. Kohn, T. Horikoshi, and T. Nakatsubo, Soil carbon cycling at a black spruce (*Picea mariana*) forest stand in Saskatchewan, Canada, *J. Geophys. Res.*, 102, 28,785-28,793, 1997.
- Pattey, E., R.L. Desjardins, and G. St-Amour, Mass and energy exchanges over a black spruce forest during key periods of BOREAS 1994, *J. Geophys. Res.*, 102, 28,967-28,975, 1997.
- Peck, E.L., T.R. Carroll, R. Maxson, B. Goodison, and J. Metcalfe, Variability of soil moisture near flux towers in the BOREAS southern study area, *J. Geophys. Res.*, 102, 29,379-29,388, 1997.
- Proctor, M.C.F., Physiological ecology: Water relations, light and temperature responses, carbon balance, in *Bryophyte Ecology*, edited by A.J.E. Smith, pp. 333-381, Chapman and Hall, 1982.
- Ryan, M.G., M.B. Lavigne, and S.T. Gower, Annual cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate, *J. Geophys. Res.*, 102, 28,871-28,883, 1997.
- Schubert, K.R. (Ed.), *The Energetics of Biological Nitrogen Fixation*, 30 pp., Am. Soc. Plant Physiol., Rockville, Md., 1982.
- Sellers, P.J., F.G. Hall, and BOREAS members, BOREAS in 1997: Experiment review, scientific results, and future directions, *J. Geophys. Res.*, 102, 28,731-28,769, 1997.
- Shulten, H.-R., and M. Schnitzer, Chemical model structures for soil organic matter and soils, *Soil Sci.*, 162, 115-130, 1997.
- Steele, S.J., S.T. Gower, J.G. Vogel, and J.M. Norman, Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada, *Tree Physiol.*, 17, 577-587, 1997.
- Thornley, J.H., Shoot:root allocation with respect to C, N and P: an investigation and comparison of resistance and teleonomic models, *Ann. Bot.*, 75, 391-405, 1995.
- Trofym, J.A., C.M. Preston, and C.E. Prescott, Litter quality and its potential effect on decay rates of materials from Canadian forests, *Water Air Soil Poll.*, 82, 215-226, 1995.
- Troth, J.L., J. Deneke, and L.M. Brown, Upland aspen/birch and black spruce stands and their soil properties in interior Alaska, *For. Sci.*, 22, 33-44, 1976.

J.A. Berry, Department of Plant Biology, Carnegie Institution of Washington, Stanford, California.

R.G. Grant, Department of Renewable Resources, University of Alberta, Canada T6G 2E1 (robert.grant@ualberta.ca).

S.E. Hale, P.G. Jarvis, J.M. Massheder, J.B. Moncrieff, M. Rayment, and S.L. Scott, Institute of Ecology and Resource Management, University of Edinburgh, Edinburgh, Scotland.

(Received May 24, 2000; revised August 19, 2000; accepted August 24, 2000.)