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Modelling temporal variability in the carbon balance of a spruce/moss boreal forest

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Abstract

A model of the daily carbon balance of a black spruce/feathermoss boreal forest ecosystem was developed and results compared to preliminary data from the 1994 BOREAS field campaign in northern Manitoba, Canada. The model, driven by daily weather conditions, simulated daily soil climate status (temperature and moisture profiles), spruce photosynthesis and respiration, moss photosynthesis and respiration, and litter decomposition. Model agreement with preliminary field data was good for net ecosystem exchange (NEE), capturing both the asymmetrical seasonality and short-term variability. During the growing season simulated daily NEE ranged from -4 g C m^{-2} d^{-1} (carbon uptake by ecosystem) to $+2$ g C m^{-2} d^{-1} (carbon flux to atmosphere), with fluctuations from day to day. In the early winter simulated NEE values were $+0.5$ g C m^{-2} d^{-1}, dropping to $+0.2$ g C m^{-2} d^{-1} in mid-winter. Simulated soil respiration during the growing season ($+1$ to $+5$ g C m^{-2} d^{-1}) was dominated by metabolic respiration of the live moss, with litter decomposition usually contributing less than 30% and live spruce root respiration less than 10% of the total. Both spruce and moss net primary productivity (NPP) rates were higher in early summer than late summer. Simulated annual NEE for 1994 was -51 g C m^{-2} y^{-1}, with 83% going into tree growth and 17% into the soil carbon accumulation. Moss NPP (58 g C m^{-2} y^{-1}) was considered to be litter (i.e. soil carbon input; no net increase in live moss biomass). Ecosystem respiration during the snow-covered season (84 g C m^{-2}) was 58% of the growing season net carbon uptake. A simulation of the same site for 1968–1989 showed $\approx$ 10–20% year-to-year variability in heterotrophic respiration (mean of $+113$ g C m^{-2} y^{-1}). Moss NPP ranged from 19 to 114 g C m^{-2} y^{-1}; spruce NPP from 81 to 150 g C m^{-2} y^{-1}; spruce growth (NPP minus litterfall) from 34 to 103 g C m^{-2} y^{-1}; NEE ranged from $+37$ to -142 g C m^{-2} y^{-1}. Values for these carbon balance terms in 1994 were slightly smaller than the 1969–89 means. Higher ecosystem productivity years (more negative NEE) generally had early springs and relatively wet summers; lower productivity years had late springs and relatively dry summers.

Keywords: black spruce, BOREAS, ecosystem model, interannual variability, moss, primary production

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Introduction

Current analyses of the global carbon budget indicate that the terrestrial biosphere is presently a significant net

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sink for carbon (e.g. Siegenthaler & Sarmiento 1993); several recent studies locate this terrestrial sink in temperate and/or boreal forests (e.g. Tans et al. 1990; Enting & Mansbridge 1991; Dai & Fung 1993; Ciais et al. 1995; Denning et al. 1995), but at this point there are not enough field data to demonstrate this. Given the large pool of carbon in boreal soils (about 200 × 10^{15} g C) and the fact

that much of their area was glaciated 14 000 years ago, these forests must have been a net sink for carbon over the past several millennia (Billings 1987). However, Oechel *et al.* (1993) report that the tundra on North Slope of Alaska is currently a source of carbon to the atmosphere, and suggest that this is due to recent climatic warming, which has increased active (thaw) layer thicknesses and enhanced regional drainage, lowering soil moisture contents and thus enhancing soil respiration. Projections for changes in the carbon balance of high latitude terrestrial ecosystems due to climate change are uncertain because of the interacting effects of temperature, moisture, and elevated CO_2 on productivity, decomposition, and nutrient cycling (e.g. Oechel & Billings 1992). Questions about the carbon balance of the boreal forest and its sensitivity to climate have motivated a large, international field campaign in the Canadian boreal forest in 1994 (Sellers *et al.* 1991; Sellers *et al.* 1995). The 1994 BOREAS (Boreal Ecosystem Atmosphere Study) campaign has generated a rich data set of biosphere-atmosphere exchange fluxes (carbon, water, energy) and ecological and hydrological properties for several characteristic boreal ecosystems (mature black spruce, mature jack pine, young jack pine, mature aspen, fen, and beaver pond).

Forests with a black spruce (*Picea mariana*) tree canopy and significant (near 100%) bryophyte ground vegetation cover of mosses (generally *Pleurozium schreberi, Hylocomium splendens,* or *Sphagnum spp.*) are a major component of the global boreal forest (Larsen 1980). Earlier field work in Alaskan black spruce stands showed that the productivity of the ground-cover moss vegetation was comparable to that of the black spruce (e.g. Van Cleve *et al.* 1983; Oechel & Van Cleve 1986), and that soil climate (temperature and moisture) exerted a significant influence on ecosystem dynamics (e.g. Van Cleve & Yarie 1986). Process-level modeling of boreal ecosystem carbon dynamics by Bonan (1991a, 1992, 1993) stressed the importance of soil temperature controls on ecosystem productivity, incorporated the role of the moss layer, and illustrated some of the seasonal dynamics of net ecosystem productivity. The model presented here has a similar structure to Bonan's daily time-step boreal forest model (Bonan 1991a, 1991b, 1993), but with different algorithms for the model processes, and with an independent data set to test model performance. Other process-level models applied to the boreal forest, such as FOREST-BGC/BIOME-BGC (Running & Coughlan 1988; Hunt & Running 1992) and the Frankfurt Biosphere Model (e.g. Lüdeke *et al.* 1995), have not addressed the role of moss in the ecosystem carbon balance.

In anticipation of the field data from the BOREAS campaign, we developed a daily time-step, ecosystem carbon balance model of spruce/moss boreal ecosystems.

This model was developed using data and insights from previous field work in other boreal regions (see Tables 2, 3 and 5), building upon earlier ecosystem modeling work of Aber & Federer (1992) and Frolking & Crill (1994). The goal was to develop a model independent of BOREAS measurements, which could then be tested against BOREAS data. Such a model can then address questions that are difficult and/or expensive to address experimentally (e.g. interannual variability in ecosystem productivity), and, through its results, can pose questions for future field studies (e.g. partitioning of total soil respiration into decomposition, root respiration, and moss respiration; dominant controls on seasonal and interannual variability in ecosystem productivity).

The model consisted of four components: (i) soil climate, which exerts controls on the dynamics of ecosystem productivity and respiration; (ii) tree photosynthesis and respiration; (iii) moss photosynthesis and respiration; and (iv) litter decomposition and associated heterotrophic respiration. The soil climate component of the model was based on the peatland soil climate model of Frolking & Crill (1994). The tree canopy component of the model carbon balance was a daily time-step version of the PnET model (Aber & Federer 1992; Aber *et al.* 1996). A similar photosynthesis and respiration model was developed for the moss, based on published physiological behaviour of feathermosses. The decomposition component determined heterotrophic respiration as a function of litter age and soil temperature and moisture. The model operated on a daily time-step and considered only short-term simulations. It ignored features of the forest carbon balance that are important in longer scenarios (e.g. wood growth and storage, limb turnover, tree mortality, changing nutrient constraints on productivity, fire). The model simulated tree gross and net photosynthesis, wood respiration, live root respiration, moss gross and net photosynthesis, heterotrophic respiration (decomposition of root litter, young needle and moss litter, and humus). These values were combined to generate predictions of total site net ecosystem exchange of carbon (NEE), total soil dark respiration (live roots + heterotrophs + live moss), spruce and moss net productivity, and net carbon accumulation in the soil.

Model results were compared with BOREAS field measurements from a black spruce/moss stand near Thompson, Manitoba. These independent data sets tested model performance in soil temperature and moisture profile dynamics, soil respiration, and net ecosystem carbon exchange. Model validation with independent data is an essential component of ecosystem modeling; the degree of success a model has in capturing observed behaviours has several implications: (i) it can illuminate model deficiencies, such as neglected ecosystem components or processes, and/or poorly functioning algorithms;

Table 1 Model parameters—site description

Parameter	Value	Units	Description	NEE Sensitivity[1]	Reference/source[2]
organic mass	24000	g m^{-2}	total organic layer mass	20	site data (Harden et al., unpublished)
z$_{moss}$	3	cm	live moss layer thickness	19	site data (Harden et al., unpublished)
FM$_{max}$	444	g m^{-2}	maximum foliar biomass	36	site data (Gower et al., unpublished)
FM$_{min}$	392.5	g m^{-2}	minimum foliar biomass	18	site data & Hom and Oechel, 1983
S$_v$	0.0088	m^3 m^{-2}	sapwood volume	13	site data (Gower et al., unpublished)
C$_{root}$	100	g C m^{-2}	fine root carbon biomass	13	R. Ruess, personal communication

1, Parameters raised and lowered 20%. Value is average magnitude of change (%) in total ecosystem NEE for the two sensitivity runs.
2, Unpublished data is preliminary site data from the BOREAS experiment.

(ii) it can address the issue of generalizability of ecophysiological parameterizations across broad landscapes, such as the global boreal forest; (iii) it can point to areas where field data (for parameterization or validation) are insufficient; and (iv) it will influence how much confidence should be put in model extrapolations (into the past or future).

Model description

Soil profile

In this discussion, the soil comprises the ground bryophyte vegetation (live moss), the litter/peat layer (no mineral soil content) below this ground vegetation, and the underlying mineral soil; the 'soil' surface is the top of the live moss. The model was one-dimensional (vertical) and considered the soil as a collection of layers. The live (green) moss layer was fixed at 3 cm thick. Below this was a layer of relatively undecomposed litter (here called the 'litter' layer). Litter layer mass and thickness were determined by the decomposability of the litter and the average annual litterfall rate (details below) and an assigned bulk density (0.075 g cm^{-3}). Below this was a humus/peat layer, consisting of well-decomposed and slowly decomposing older litter (here called the 'humus' layer). Humus layer mass and thickness were determined by the difference between the site's total organic layer mass (see Table 1) and the masses of the live moss and litter layers, and an assigned bulk density (0.1 g cm^{-3}). Below these organic layers was the mineral soil, which was divided into several layers in the soil climate submodel. In the model, organic matter input to the mineral soil was by spruce fine root turnover only.

Soil climate

Inputs

The model was driven by daily weather data and generated daily profiles of temperature, water content, and ice

content in the soil column (to 1.6 m in the mineral soil). Ideally, the input data set would include daily maximum and minimum air temperatures, daily total precipitation, daily mean relative humidity (rh), and daylight average photosynthetically active radiation (PAR) intensity (rh and PAR are used for calculating photosynthesis). The minimum data set needed was maximum and minimum air temperatures and total precipitation. Daytime, nighttime, and daily average temperatures were calculated as

$$T_{avg} = (T_{max} + T_{min})/2$$
$$T_{day} = (T_{max} + T_{avg})/2 \qquad (1)$$
$$T_{night} = (T_{avg} + T_{min})/2.$$

If relative humidity data were available, daily vapour pressure deficit (VPD) was calculated as the saturation vapor pressure at T_{day} times one minus the relative humidity; otherwise VPD was the difference between saturated vapor pressures at T_{day} and T_{min}. For the site modelled in this paper, PAR data were collected throughout most of the 1994 BOREAS campaign. Simulations of other years used a synthetic PAR field generated from the observed (1994) relationship between PAR (in μE m^{-2} s^{-1}) and diurnal temperature range ($\Delta T = T_{max} - T_{min}$) for days with T_{max} greater than 0°C (Fig. 1a). On days with T_{max} less than 0°C (which are likely to be photosynthetically inactive), PAR was determined by a sinusoidal fit to the 1994 cold season minimum observed PAR data augmented by a diurnal temperature range factor (Fig. 1b). Thus, if PAR data were unavailable

$$PAR = \begin{cases} 90.3 + 30.3 \cdot \Delta T & \text{if } T_{max} \\ 650 \left(\dfrac{1.25 - \sin(2\pi \bar{d}/365 - 1.9)}{2.25} \right) + \dfrac{\Delta T^2}{2} & \text{if } T_{max}, (2) \end{cases}$$

where $\bar{d}$ is the day of year. For wider application of the model, a more general PAR function will be developed. Precipitation was partitioned into rain and snow following the method of Federer (1995); all rain if T_{min} was greater than the cut-off temperature, T_{rs} (equal to –0.5°C;

Nipawan and Nelson House PAR data 1994
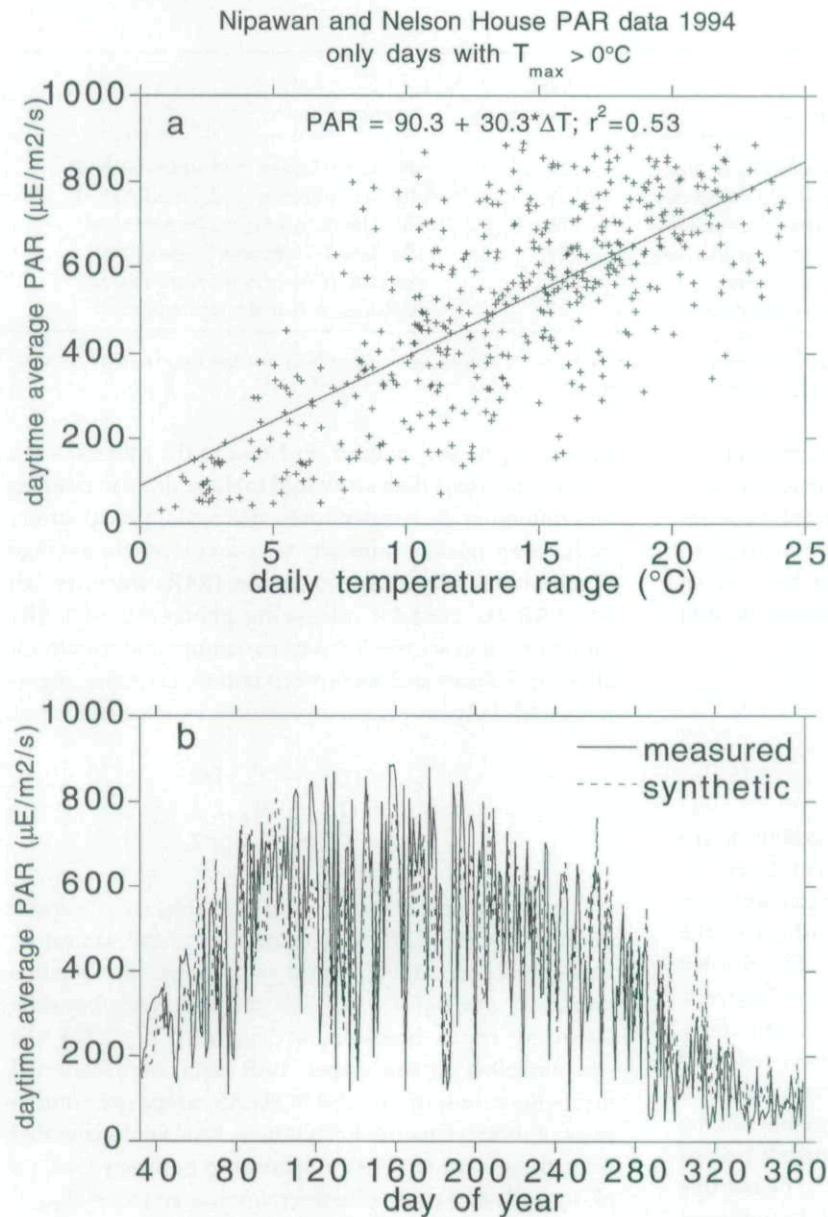## only days with T$_{max}$ > 0°C

Fig. 1 (a) Daylight average PAR vs. daily air temperature range (midnight to midnight), including only those days with T_{max} greater than 0°C. The linear fit was used to generate synthetic PAR values for simulations of other years (except for cold days, see Eq. 2 in the text). **(b)** A comparison of the observed and synthetic (Eq. 2 in text) daylight average PAR values for 1994.

Federer 1995), all snow if T_{max} was less than T_{rs}, or else a mixture of rain and snow with a snow fraction, S_f, of

$$S_f = \frac{T_{rs} - T_{min}}{T_{max} - T_{min}}. \tag{3}$$

Heat

Soil temperature was modelled in one (vertical) dimension by standard soil physics methods (e.g. Campbell 1985). Daily mean air temperature was applied at the soil or snowpack surface, and a finite difference approach was used to calculate heat diffusion in the soil. Although the moss surface can get much warmer than the air

temperature (e.g. Proctor 1982), this happens only if the moss is quite dry (with little or no evaporative cooling) and exposed to direct sunlight. The surface can then get hot ($\approx$ 40–50°C) because the moss has low thermal mass and low thermal conductivity, both due to low water content. These thermal properties also imply that little heat energy is actually stored in the moss, and that little effect will be felt deeper in the organic horizon where the water content is generally higher. Therefore, ignoring this heating above air temperature should cause only a small error in the overall soil climate. Freezing and thawing were calculated using the apparent heat capacity method (e.g. Lunardini 1981); the percentage of soil water that was frozen increased linearly from 0% at 0°C to

Table 2 Model parameters— soil climate

Parameter	Value	Units	Description	NEE Sensitivity[1]	Reference/source
Organic Soil					
ρ_m	0.033	g cm^{-3}	moss bulk density	35	Barney & Van Cleve 1973
ρ_l	0.075	g cm^{-3}	litter bulk density	11	Golding & Stanton 1972; Dyrness & Grigal 1979; Pritchett & Fisher 1987
ρ_h	0.1	g cm^{-3}	humus bulk density	16	Golding & Stanton 1972; Dyrness & Grigal 1979; Pritchett & Fisher 1987
W_{minm}	0.4	g water g^{-1} dry	moss min. water content	1	Skre et al. 1983; Busby & Whitfield 1978
W_{minl}	0.1	g water g^{-1} dry	litter min. water content	0	Reynolds & Knight 1973; Waring & Schlesinger 1985
W_{minh}	0.25	g water g^{-1} dry	humus min. water content	0	Reynolds & Knight 1973; Waring & Schlesinger 1985
W^*_m	1.7	g water g^{-1} dry	moss moderate water	1	-
W^*_l	1.0	g water g^{-1} dry	litter moderate water	1	-
W^*_h	2.0	g water g^{-1} dry	humus moderate water	16	-
W_{fcm}	5.25	g water g^{-1} dry	moss field capacity	17	Skre et al. 1983; Busby & Whitfield 1978
W_{fcl}	3.0	g water g^{-1} dry	litter field capacity	1	Reynolds & Knight 1973; Golding & Stanton 1972; Waring & Schlesinger 1985
W_{fch}	3.0	g water g^{-1} dry	humus field capacity	31	Reynolds & Knight 1973; Golding & Stanton 1972; Waring & Schlesinger 1985
τ^2_m	1.5	day	moss drying constant	2	Skre et al. 1983; Busby et al 1978
τ^2_l	3.0	day	litter drying constant	1	Reynolds & Knight 1973
τ^2_h	4.0	day	humus drying constant	0	Reynolds & Knight 1973
lag^3_l	2	day	litter lag time for drying	2	Reynolds & Knight 1973
lag^3_h	4	day	humus lag time for drying	3	Reynolds & Knight 1973
Mineral Soil (clay)					
k	2	mm d^{-1}	hydr. cond. at field cap.	2	Federer 1995
W_{min}	0.22	vol. water content	minimum water content	4	Federer 1995
W_{fc}	0.36	vol. water content	field capacity	19	Federer 1995
W_{sat}	0.45	vol. water content	maximum water content	19	Federer 1995
Snow					
ρ_{max}	0.30	g cm^{-3}	max. snow density	6	Dingman 1994
ρ_{min}	0.1	g cm^{-3}	min. snow density	11	Dingman 1994

1, Parameters raised and lowered 20%. Value is average magnitude of change (%) in total ecosystem NEE for the two sensitivity runs.
2, Parameters raised and lowered by one day. 3, Parameters raised and lowered by two days.

100% at −1°C. Soil thermal properties were a function of bulk density, organic matter content, and liquid and frozen water content. A more complete discussion of the methodology is given in Frolking & Crill (1994). See Table 2 for thermal and hydraulic parameters.

Water

Liquid water inputs to the soil were rain (after interception loss to the tree canopy) and snowmelt. Water losses from the soil were transpiration by trees, evaporation of water intercepted by the moss, litter, and humus layers, run-off from a saturated or frozen soil profile, and drainage from the bottom of the modelled profile.

Tree canopy interception Tree canopy interception was modelled as a function of canopy water-holding capacity, with different capacities for rain and snow. Interception capacities (in centimeters of water) were calculated (following Federer 1995) as

$$I = \begin{cases} 0.015\,(LAI + SAI) & \text{for rain} \\ 0.04\,LAI + 0.06\,SAI & \text{for snow,} \end{cases} \tag{4}$$

where *LAI* and *SAI* were area indices of leaves and stems. All intercepted rainfall was assumed to be lost as evaporation. Intercepted snow was assumed to be lost to sublimation at 20% per day.

Transpiration Daily transpiration was calculated by multiplying daily net spruce photosynthesis by its water-use efficiency (Aber & Federer 1992). Transpiration water loss was distributed in the litter, humus, and mineral soil layers based on the tree root distribution and water availability. Root distribution was prescribed as 80% in the litter and humus horizons (split in proportion to respective layer thicknesses) and 20% in the top 10 cm of the mineral soil (Tryon & Chapin 1983). Water availability to tree roots for transpiration in each layer was reduced by the layer's fractional ice content.

Moss/Organic Horizon Water Dynamics Mosses and peats have very low bulk densities, very high porosities, and very high water-holding capacities (e.g. Boelter & Verry 1978). In the model, each organic layer (living moss, litter, and humus) was given four key water contents (minimum, moderate, field capacity, and saturation, see Table 2). At the minimum water content all water loss stopped; when the water content in a layer rose above the moderate water content, additional water inputs were split between that layer and the layer below (i.e. partial drainage upon wetting); water content above the field capacity was immediately drained to lower layers or the mineral soil, unless underlying layers were frozen, under which condition a layer's water content could rise toward saturation. All water added that would raise the water content above saturation was immediately lost as runoff/drainage. There was no mechanism for upward water movement in the soil, nor for horizontal inflow.

As mosses are not vascular plants, they lose water only by evaporation. Field studies have shown that, in boreal forests, mosses wetted by a storm usually remain wet only for a few days to a week (Busby & Whitfield 1978; Skre *et al.* 1983). Evaporation water loss from moss, litter, and humus layers was modeled as an exponential decay of layer water content from its value at the end of the storm to its minimum water content value

$$W(t) = \begin{cases} W_0 & \text{if } t < lag \\ W_{min} + (W_0 - W_{min})e^{-(t-lag)/\tau}, & \text{if } t \geq lag \end{cases} \tag{5}$$

where W_0 is the water content at the end of the storm, t is the time in days since the rainy day, *lag* is a delay before drying begins (days), and τ is a characteristic drying time of the layer (days), adjusted for time of year as

$$\tau = \tau_0\left(1 + 5\left(\frac{doy - 200}{200}\right)^2\right), \tag{6}$$

where τ_0 is the drying time in mid-summer (parameter values in Table 2). If there was a snow cover (greater than 1 cm) no evaporation occurred from the moss, litter, or humus layers. In addition, the litter and humus layers lost water from transpiration via tree roots. Total loss from transpiration plus evaporation was limited to the daily potential evapotranspiration as calculated with the Thornthwaite equation (Dunne & Leopold 1978), but could be less if constrained by water availability.

Mineral soil water dynamics Since the site to be modeled had a very high ground coverage of moss and a thick surface organic horizon (27 cm), evaporation from the mineral soil was probably negligible. Water flow in the mineral soil was modelled as gravity drainage only. Flow rates, Q, from one layer to the next lower layer were given by

$$Q_{i \to j} = \sqrt{(k_i k_j)}, \tag{7}$$

where k_i and k_j are the hydraulic conductivities of each layer, calculated as a function of soil texture and water content (Federer 1995). Drainage from the bottom of the profile equaled the hydraulic conductivity of the lowest layer. If the soil was partly to completely frozen, the hydraulic conductivity lowered with the fractional ice content

$$k_i = \hat{k}_i(1 - ice_i), \tag{8}$$

where $\hat{k}_i$ is the hydraulic conductivity with no ice present, and ice_i is the layer's fractional ice content. The mineral soil also lost water via transpiration in the zone where roots were present (0–10 cm). See Table 2 for hydraulic parameters.

Snowpack dynamics The model kept track of the snowpack water content by simple water balance (change equaled daily snowfall minus daily snow melt). The snowpack density was a function of time of year, rising from 0.1 g cm^{-3} in the early winter to 0.3 g cm^{-3} by spring, following data summarized in Dingman (1994). Snow melt was a function of daylength (as a proxy for time of year and radiation loading) and a melt temperature, T_{melt} (Dingman 1994). It occurred whenever the maximum daily air temperature was greater than 0°C. The melt temperature was equal to the mean daily air temperature if it was greater than 0.5°C, otherwise it was set at 0.5°C. Snow melt (centimeters per day) was then given as (Dingman 1994)

$$S_m = 0.0945 T_{melt} dl, \tag{9}$$

where dl is the fractional daylight length (12 hours = 1.0). The snowpack could hold liquid water up to 6% of its snow void volume (snow density divided by snow depth). Melt or rainwater greater than this amount drained into the underlying organic layer (Dingman 1994), unless that layer was frozen or saturated.

Tree photosynthesis and respiration

Canopy photosynthesis

The carbon and water balances of the tree canopy were calculated following a daily time step version of the PnET model (Aber & Federer 1992; Aber et al. 1996). Briefly, given a prescribed potential photosynthesis, actual photosynthesis was calculated as the potential value modified by air temperature, light, VPD, and soil water availability factors (see Fig. 2a–d). Canopy transpiration equalled total canopy photosynthesis times spruce water-use efficiency (a function of VPD). Maximum canopy biomass was an input parameter. The timing of needle growth was determined by the accumulated growing degree days (Table 3). Senescence and needle drop were allowed after a specified date, when needles were dropped that could not maintain a positive carbon balance. Annual needle loss was set at 11.6% of needle biomass (Hom & Oechel 1983).

For this version of the PnET model (black spruce only), the maximum photosynthetic rate was set to 18.9 nmol CO_2 g^{-1} s^{-1} (Hom & Oechel 1983). Maximum foliar biomass was set at 444 g m^{-2}. Needle retention times of 10 or more years are not uncommon in black spruce (Hom & Oechel 1983). As the needles age, their capacity for photosynthesis declines to about half the fresh needle value after 10 years; during the same period needle nitrogen content drops to about 75% of its initial value (Hom & Oechel 1983). Data on needle photosynthetic capacity, nitrogen content, and age class distribution (Hom & Oechel 1983) were used to determine a canopy-averaged, needle-age factor of 0.855 for photosynthesis and 0.945 for respiration (see Table 4).

Tree respiration

Leaf respiration was calculated as in the daily time-step version of PnET. Respiration was a function of air temperature (day and night), leaf biomass, and a base respiration rate, set to 10% of maximum net photosynthesis rate at the optimal temperature for photosynthesis (15°C for spruce) (Aber & Federer 1992). Root respiration, R_{root}, was calculated as a function of root carbon content per unit ground area in moles C per square metre, C_{root}, root C:N, and root (soil) temperature (Ryan 1991)

$$R_{root} = \frac{0.0106 \, C_{root}}{(C:N)_{root}} \, Q_{10,r} \left(\frac{T_{root}}{10} \right), \tag{10}$$

with a Q_{10} value of 1.8 (Ryan 1991). Note that (10) gives the root respiration value in mol CO_2 h^{-1} m^{-2}. Woody tissue respiration was calculated as a function of sapwood volume per unit ground area, S_v, and air temperature (Ryan et al. 1995)

$$R_{wood} = 7.5 \cdot S_v \cdot Q_{10,s} \left(\frac{T_{air} - 10}{10} \right), \tag{11}$$

with a Q_{10} value of 1.7 (Ryan et al. 1995). Note that (11) gives the sapwood respiration value in µmol CO_2 s^{-1} m^{-2}. Root biomass and sapwood volume were site-specific input parameters, and were considered constant throughout each simulation (Table 3).

Moss photosynthesis and respiration

Light extinction and photosynthesizing depth

Light intensity attenuates as it moves down into a moss canopy, following a simple Beer's Law exponential decay (Skre et al. 1983; Longton 1988)

$$I = I_0 e^{-k\rho_b z}, \tag{12}$$

where I_0 is the light intensity at the moss surface, ρ_b is the moss bulk density (33.3 kg m^{-3}), z is depth into the moss canopy (m), and k is the light extinction coefficient (2.8 m^2 kg^{-1}). At 0.03 m depth into feathermoss, (12) reduces light intensity to 6.1% of its value at the surface of the moss. This was chosen as the live, green (photosynthesizing) canopy depth each spring.

Photosynthesis and respiration

Moss photosynthesis was calculated daily as a maximum rate (1.0 mg CO_2 g^{-1} h^{-1}), reduced by light availability and model-generated temperature and moisture conditions (see Fig. 2a,b,e and Table 3), and multiplied by daylength. The green moss 'canopy' was considered to have a uniform moisture content, and a linear temperature gradient from the air temperature at the surface (when not snow covered) to the modelled temperature at the bottom of the live moss. Moss temperatures can get much higher than the local air temperature if they are dry and exposed to the sun (Proctor 1982). However, when mosses are dry, both photosynthesis and respiration are very low (e.g. Proctor 1982), so the temperature effects will have little influence on the carbon balance (unless conditions become lethal due
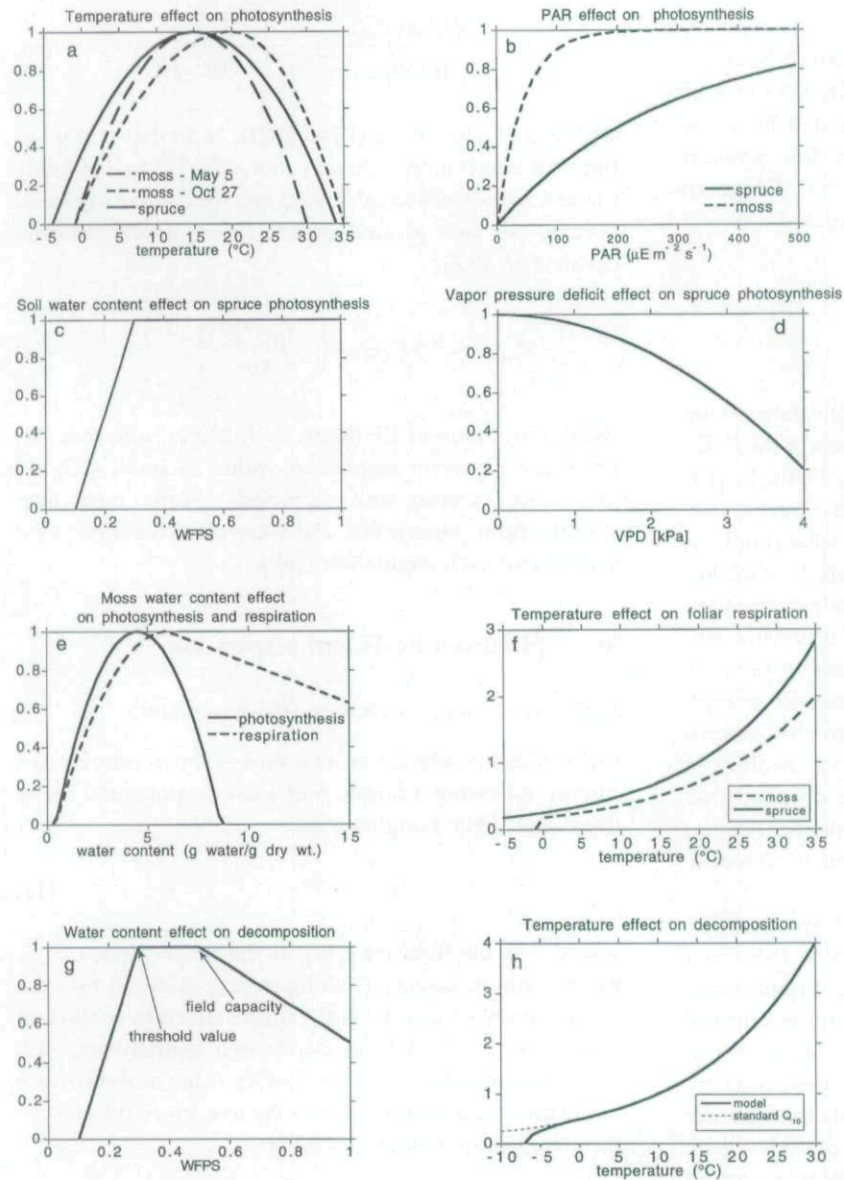
Fig. 2 Ecophysiological responses to biophysical drivers were based on literature values; parameter values and references are listed in Tables 2, 3 and 5 and in Aber and Federer (1992). Tables 2, 3 and 5 also report overall model sensitivity to the parameters. (a) Air temperature effect on spruce photosynthesis (solid line) and moss temperature effect on moss photosynthesis at the beginning (long dashes) and the end of the growing season (short dashes). The optimal temperature for moss photosynthesis increased at a constant rate throughout the growing season. (b) Photosynthetically active radiation (PAR) influence on photosynthesis for spruce (solid line) and moss (dashed line). (c) Effect of soil water content on spruce photosynthesis; curve shape is identical for all layers with roots (litter, humus, and 0–10 cm mineral soil) but water-filled pore space (WFPS) values shown in plot are for the litter layer. (d) Effect of vapour pressure deficit (VPD) on spruce photosynthesis. (e) Effect of moss water content on moss photosynthesis (solid line) and metabolic respiration (dashed line). (f) Effect of air temperature spruce respiration (dashed line) and moss temperature on moss respiration (solid line). (g) Effect of soil water content on decomposition. (h) Effect of soil temperature on litter decomposition (solid line) and generic exponential dependence (Q_{10}) model (dashed line).

to extended drought and heat – this was not modelled). Respiration was calculated for the day and night separately, with the moss surface temperature set to T_{day} or T_{night} (Eq. 1), again with a base rate (0.175 mg CO_2 g^{-1} h^{-1}), modified by model generated temperature and moisture conditions (see Fig. 2e,f and Table 3), and multiplied by day and night lengths. Both photosynthesis and respiration were calculated per unit weight for 10 layers down the moss canopy, adjusting light intensity and temperature with each step. Moss photosynthesis under the snowpack was possible if moss temperatures and light levels permitted. Light attenuation in the snowpack was modeled as exponential decay, falling to 37% (e^{-1}) at 10 cm (Longton 1988).

Snow covered moss also respired if the moss was warmer than –1°C.

Photosynthesis and respiration rates have been observed to decline with age or depth in the green moss profile (Oechel & Van Cleve 1986). This was modeled as full rates for the top 1/3 of the live moss canopy, 75% rates for the middle third, and 50% rates for the bottom third.

Decomposition and soil respiration

Litter inputs

Black spruce needle litter was considered to fall through the live moss layer to the top of the litter layer and

Table 3 Model parameters— vegetation carbon balance

Parameter	Value	Units	Description	NEE Sensitivity[1]	Reference/Source
Photosynthesis Tree[2]					
A_{max}	18.9	nmole g^{-1} s^{-1}	max. net photosynthesis	66	Hom & Oechel 1983
GDD_{start}	300	degree days (°C)	DD to start foliar growth	0	–
GDD_{end}	800	degree days (°C)	DD to end foliar growth	1	–
SN_{start}	270	yearday	earliest day to drop needles	5	–
Feathermoss					
A_{max}	1.0	mg CO2 g^{-1} h^{-1}	max. net photosynthesis	16	Skre & Oechel 1981; Green & Lange 1994
T_{opt}	15→20	°C	optimal temperature	14/3[3]	Skre & Oechel 1981
$T_{min,psn}$	-1	°C	minimum temperature	0[4]	–
W_{opt}	4.5	g water g^{-1} dry	optimal water content	58	Skre & Oechel 1981; Busby & Whitfield 1978
W_{min}	0.25	g water g^{-1} dry	minimum water content	0	Skre et al. 1983; Busby & Whitfield 1978
halfsat	40	μE PAR m^{-2} s^{-1}	PAR half saturation	51	Busby & Whitfield 1978
Respiration Tree[1]					
R_r	0.0106	mol C mol^{-1} N h^{-1}	root resp. rate (20°C)	13	Ryan 1991
$Q_{10,r}$	1.8		root Q_{10} temp. response	26	Ryan 1991
$C:N_{root}$	45		black spruce fine root C:N	13	Hendricks 1994
R_{sw}	15	μmol C m^{-3} s^{-1}	sapwood resp. rate (10°C)	13	Ryan et al 1995
$Q_{10,sw}$	1.7		sapwood Q_{10} response	4	Ryan et al 1995
Feathermoss					
R	0.175	mg CO2 g^{-1} h^{-1}	moss resp. rate (20°C)	37	Skre & Oechel 1981
Q_{10}	1.75		exponential response - temp	94	Skre & Oechel 1981; Oechel & Van Cleve 1986
W_{opt}	6.0	g water g^{-1} dry	optimal water content	65	Skre & Oechel 1981; Dilks & Proctor 1979

1, Parameters raised and lowered 20%. Value is average magnitude of change (%) in total ecosystem NEE for the two sensitivity runs. 2, Only values different Aber & Federer 1992. 3, Sensitivity to 20% change in initial optimum (15°C)/temperature increase (5°C). 4, Parameter raised and lowered 1°C.

Table 4 Needle Age effect on photosynthesis and respiration

Needle age [y]	Fractional mass[1]	Relative A_{max}[3]	Relative N content[2]	Effective A_{max}[2]	Effective respiration[4]
0	0.116	1.000	1.000	0.116	0.116
1	0.116	1.000	1.000	0.116	0.116
2	0.116	1.000	1.000	0.116	0.116
3	0.110	1.000	1.000	0.110	0.110
4	0.110	0.925	1.000	0.102	0.110
5	0.110	0.850	1.000	0.093	0.110
6	0.098	0.775	0.950	0.076	0.093
7	0.081	0.700	0.900	0.057	0.073
8	0.058	0.625	0.850	0.036	0.049
9	0.035	0.550	0.800	0.019	0.028
10	0.023	0.475	0.750	0.011	0.017
11	0.012	0.400	0.700	0.005	0.008
12	0.012	0.330	0.700	0.004	0.008
13	0.006	0.330	0.680	0.002	0.004
Total	1.000			0.855	0.945

[1]Based on occurrence frequency in Hom & Oechel (1983). [2]Based on data in Hom & Oechel (1983). [3]Cohort effective A_{max} = (cohort fractional mass) × (cohort relative A_{max}). [4]Cohort effective Respiration = (cohort fractional mass) × (cohort relative N content).

joined the year's moss litter as an annual litter cohort. Since live (green) moss depth was fixed, moss 'litterfall' was equal to net biomass accumulation over the growing season (if positive, otherwise moss litter was zero). Root litter inputs were distributed in depth based on the prescribed root distribution and root biomass turnover rates. Live fine root turnover was fixed at 25% per year. Fine root litter mass was initialized at 166 g C m^{-2}; this put it in steady state with the prescribed input of 25 g C m^{-2} and an average annual mass loss rate of 15% (Berg *et al.* 1993). All litterfall occurred in the autumn.

Decomposition

A number of studies of long-term litter decomposition have shown that the fractional mass loss rate tends to decline as the litter ages (e.g. Swift *et al.* 1979). This could be due to early, rapid loss of more soluble components of the litter and/or to gradual changes in the litter composition (e.g. nutrient, cellulose, or lignin content) and hence decomposability (e.g. Swift *et al.* 1979). For several high-latitude species (*Calluna* stems and shoots, *Eriophorum* leaves, and *Rubus* leaves) Heal *et al.* (1978) found that the litter respiration rate (decomposition) declined linearly with the accumulated fractional mass loss, m^*,

$$m^* = \frac{m_0 - m}{m_0} = 1 - \frac{m}{m_0}, \tag{13}$$

where m_0 is initial mass of the litter, and m is the current litter mass. The litter respiration rate, R (in $\mu l \ O_2 \ g^{-1} \ h^{-1}$), was roughly given by

$$R(t) = R_0(1 - \alpha m^*), \tag{14}$$

where R_0 is the initial rate, α is a parameter (≈ 1.0 in their data). For decomposition in high latitude ecosystems, Bunnell *et al.* (1977) estimate that respiration accounts for almost all litter mass loss. Assuming it is the only mode of mass loss gives

$$\frac{dm}{dt} = -R(t) \cdot m = -R_0 m(1 - \alpha(1 - m/m_0)). \tag{15}$$

For $\alpha = 0$ (straight exponential decay) and $\alpha = 1.0$, there are simple solutions to (15) for the remaining litter mass as a function of time in an annual cohort

$$m(t) = \begin{cases} m_0 e^{-R_0 t} & \text{if } \alpha = 0 \\[2mm] \dfrac{m_0}{1 + R_0 t} & \text{if } \alpha = 1 \\[2mm] \dfrac{(1-\alpha)m_0}{e^{R_0(1-\alpha)t} - \alpha} & \text{if } \alpha \neq 0,1. \end{cases} \tag{16}$$

If α is greater than 1.0, the accumulated mass loss will approach an asymptote less than 100% (Berg & Ekbohm 1991), given by

$$m(t \to \infty) = m_0 \left(1 - \frac{1}{\alpha}\right). \tag{17}$$

The difference between the behaviours of the simple decay ($\alpha = 0$) and the other solutions becomes more significant after some time has elapsed (as the fractional mass loss increases). This study used $\alpha = 1$ (decomposition parameters listed in Table 5).

As cohorts age their fractional mass loss rate declines, as does their remaining mass. The product of these is the total mass loss (respiration) rate. When this fractional mass loss rate declined to 2.5% of the initial rate, the remaining cohort mass was transferred to a single humus pool, which then decayed exponentially (i.e., $\alpha_{humus} = 0$) at this final rate (as modified by soil climatic conditions; see Fig. 2 g,h). The transfer time was determined by the rate chosen for humus decomposition and the initial mass loss rate as (for $\alpha = 1$)

$$\left(\frac{dm/dt}{m}\right)^* = \frac{-R_0 m^2/m_0}{m} = \frac{-R_0 m}{m_0} =$$

$$\frac{-R_0 \left(\dfrac{m_0}{1 + R_0 t}\right)}{m_0} = \frac{-R_0}{1 + R_0 t} \tag{18}$$

so

$$t_\to = \frac{-R_0 - \left(\dfrac{dm/dt}{m}\right)^*}{R_0 \left(\dfrac{dm/dt}{m}\right)^*}. \tag{19}$$

If the litter were continuously exposed to normal surface climatic conditions and R_0 was equal to 0.15, the transfer occurred when 84% of the initial mass has been lost, after 34 years. For $\alpha = 0$ and $R_0 = 0.15$, respiration would decrease to 2.5% of the initial rate after 97.5% of the initial mass had been lost, 25 years after litterfall.

Berg et al. (1993) showed that, for a variety of sites, first year mass loss of needle litter is well correlated with annual actual evapotranspiration (AET). Using all of their data, or using their division into two subsets (Mediterranean, Central European, and North American sites; European sites exposed to Atlantic climate), both linear and exponential fits gave roughly equivalent correlations. First year mass loss rates for the six possible regressions and an AET of 325 mm y^{-1} (appropriate for BOREAS sites) ranged from 12 to 20%. This study used 15%, which was consistent with boreal litter decomposition studies of Sparrow et al. (1992), Hogg (1993), Hogg et al. (1992), Fyles & McGill (1987), Moore (1984), and Berg (1984).

Soil climate effects   Since the model calculated a daily profile of temperature (T) and moisture (W) within the litter/peat/mineral soil, the model used a base daily decomposition rate (DR_0) that was then modified by the daily soil climate conditions of each cohort, given generally as

$$R(T,W) = DR_0 f_1(W) f_2(T),\qquad(20)$$

where $f_1(W)$ is the moisture effect (Fig. 2g) and $f_2(T)$ is the temperature effect (Fig. 2h). DR_0 was determined by using long term mean daily weather data for the site, running the soil climate submodel to determine the temperature and water content of the top of the litter layer (first year cohort), finding the annual total of $R(T,W)$ by summing (20) over the year, and then normalizing it to the annual mass loss value

$$
\begin{aligned}
R_0 &= \sum_{i=1}^{365} DR_i \\[4pt]
&= \sum_{i=1}^{365} DR_0 f_1(W_i) f_2(T_i) \qquad(21)\\[4pt]
&= DR_0 \sum_{i=1}^{365} f_1(W_i) f_2(T_i)
\end{aligned}
$$

so

$$DR_0 = \frac{R_0}{\displaystyle\sum_{i=1}^{365} f_1(T_i) f_2(W_i)}.\qquad(22)$$

DR_0 was roughly equal to 0.5% of R_0. The actual daily respiration (and mass loss) rate for cohort i (or the humus layer) was then determined by the daily soil climate conditions as

$$R_i(T,W) = DR_0 \cdot f_1(T_i) \cdot f_2(W_i).\qquad(23)$$

Initializing the profile

To initialize the decomposition state of the litter/humus profile, the mass and fractional mass lost of each cohort

had to be specified. When this was done, each cohort's current mass loss rate was given by (15). The model assumed that the litter (needle + moss) deposition rate, m_0, had been constant at an average value for all past years, and that the mass loss rate had been at the mean value, R_0, each year. Each litter cohort then had a mass given by (16), and the total litter mass (all cohorts younger than the transfer time), $M(t_\rightarrow)$, was given by

$$
\begin{aligned}
M(t_\rightarrow) &= \int_0^{t_\rightarrow} m(t)\,dt \\[4pt]
&= \int_0^{t_\rightarrow} \frac{m_0}{1 + R_0 t}\,dt \qquad(24)\\[4pt]
&= \frac{m_0}{R_0}\ln(1 + R_0 t_\rightarrow).
\end{aligned}
$$

The remaining mass of the organic horizon (total mass was an input parameter) was placed in the humus pool.

Root litter decomposition

Fine root litter (fixed at 25% of total fine root biomass each year) was deposited into the soil profile in accord with root biomass distribution. Because each annual root litter cohort was distributed in space (from the top of the litter layer down into the mineral soil) it experienced a range of soil climatic conditions. Thus all root litter decomposition was modelled, like humus, as a single exponentially decaying pool (i.e. $\alpha = 0.0$ in Eq. 15), with an annual rate equal to that of fresh needle and moss litter (R_0), modified by the temperature and moisture conditions at each level in the soil profile.

Model validation

Model results were compared to field data from the 1994 BOREAS field campaign, and against data reported in the literature. The field site used for model testing was the Old Black Spruce site in the BOREAS Northern Study Area (NSA–OBS), near Thompson, Manitoba (55°52′N, 98°29′W). The site was a level stand of 75–90-y-old, 10 m-tall black spruce trees (*Picea mariana*), with a nearly complete groundcover of mosses, predominantly *Pleurozium schreberi* (a feathermoss) and *Sphagnum spp*.

A number of groups undertook field studies at the NSA–OBS site in 1994. A nearly complete meteorological record for 1994 was collected nearby by the Saskatchewan Research Council (SRC). An eddy correlation flux tower and soil temperature probes were operated by a group from Harvard University. Soil temperature and static chamber soil CO_2 flux measurements were made independently by groups from the US Geological Survey (USGS; Winston et al. 1995), McGill University, and the

University of New Hampshire (UNH). Organic horizon water contents were measured gravimetrically by a group from the University of Toronto. A group from the University of Wisconsin measured aboveground tree and leaf biomass. Field data presented here are preliminary data; the data have been checked by the field research groups, but do not represent their final analysis, nor does this work represent the complete scope of any field group's work on the BOREAS project.

Weather data A 1994 daily (midnight–midnight) weather input file (T_{max}, T_{min}, precipitation, PAR, relative humidity) was generated from the 15 minute averages collected and reported by the SRC meteorological station at Nelson House (about 9 km to the northwest of NSA–OBS). There were no data for January 1994, so temperature data came from a Canadian Atmospheric Environment Service (AES) met station at Flin Flon (about 250 km to the southwest; although temperatures were undoubtedly different at Flin Flon, model sensitivity runs showed a 0.4% decrease in annual NEE for a 3.5°C increase in air temperature for all of January and February, and a 1.5% increase in annual NEE for a 3.5°C decrease in air temperature for all of January and February); precipitation data came from January 1985, collected by AES at the Thompson airport (about 40 km to the east; Jan. 1985 precipitation was near the January mean for 1980–1989 at that site). Other missing data were filled in as follows: 1994 SRC Thompson (airport) station precipitation data were substituted for missing data for 1 February through 19 March and 1–19 November; 20–21 November precipitation were set to zero; January PAR values were determined with Equation 2. The model was then run for 4 + consecutive '1994's, starting in mid-October. This means that model Jan. 1994 conditions were influenced by October–December 1994 weather, rather than October – December 1993. Results reported are for the final 1994 simulated, though the model was quite stable. In year one of the simulation, soil respiration was about 10% higher than subsequent '1994s', implying a slight over-initialization of the litter cohort masses.

Site initialization The model site was a black spruce/moss forest. The organic horizon mass was set at 24.0 kg m^{-2} (27.1 cm thick); it was separated into 1.0 kg m^{-2} of green moss (3 cm thick); 0.2 kg m^{-2} of live fine roots and 0.33 kg m^{-2} of fine root litter, 1.72 kg m^{-2} of needle and moss litter (34 annual cohorts, with masses declining from 0.14 to 0.025 kg m^{-2}; total thickness = 2.6 cm), and 20.9 kg m^{-2} of humus (21.1 cm thick). Litter and humus masses were calculated with (24). The underlying mineral soil was a clay. In the top 10 cm of the mineral soil, the model was initialized at 0.05 kg m^{-2} of live fine roots and 0.083 kg m^{-2} of fine root litter. Sapwood volume was

0.0088 m^3 m^{-2}; maximum needle biomass was 0.444 kg m^{-2}.

Soil climate results

Soil temperatures were compared to the daily average of high-frequency data collected at five depths near the eddy-correlation flux tower, and to mid-day measurements made by the chamber flux groups at one to several week intervals for two or three soil depths (Fig. 3). Model temperatures at 5, 10, and 20 cm were generally cooler than observed by the Harvard tower group, much cooler than observed by the UNH chamber flux group, but warmer than observed by the McGill chamber flux group. These differences were most pronounced in May and June, and tended to diminish in late summer. The three temperature trajectories observed by the three groups (see 10 and 20 cm results in Fig. 3) probably span the range of behaviours that occurred at NSA–OBS, from cold (and wet) in the McGill group observations to warm (and dry) in the UNH group observations. Also, McGill and UNH measurements were mid-day values, while the tower and model numbers are daily averages. Model results were toward the cooler end of this spectrum. Heat transfer in the model soil profile is predominantly by conduction (heat convection was only considered in association with the flow of liquid water into frozen soil) so discrepancies in soil temperatures imply that model thermal diffusivities were off in the surface layers, or that other heat transfer processes were important.

Model temperatures at 5 and 10 cm were generally warmer than the tower data during Days 270–290 but were in close agreement once the snowpack formed (Day 305). During February, model temperatures were colder at 5, 10, and 20 cm than observed by the Harvard group, but warmer than observed by the USGS group (Winston *et al.* 1995). Sensitivity runs with soils held at saturation and wilting point showed the dry soils to be about 10–15°C cooler than the wet soils during the winter months, and 0–5 °C cooler in the summer months, but with an earlier and more rapid thaw. Differences in winter soil water content may account for differences in winter temperatures. The model site was specified as non-permafrost; maximum model frost depth was about 80 cm (from top of moss) and final thaw was on about Day 230.

Organic layer water contents were compared to daily gravimetric water data collected by the Toronto group (Fig. 4). They cut 16 cm × 16 cm turves into the organic layers. Adjacent turves were cut through the L, the L and F, and the L, F and H. Each turve was placed in a permeable net, removed for daily and sub-daily mass determination, and replaced. Measurements were made for about 30 days. Water mass was determined by wet weight minus the oven dry turve weight (measured at
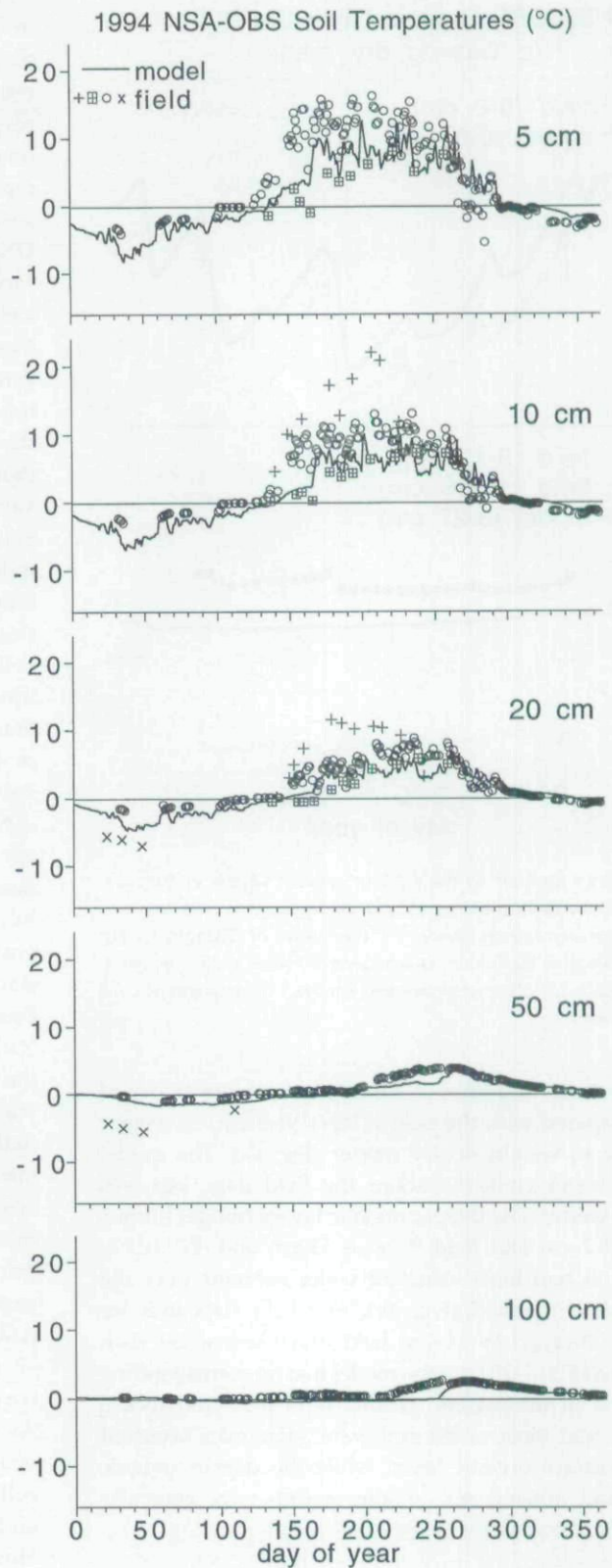
Fig. 3 Soil temperatures at five depths measured down from the top of the moss: daily average of high frequency thermocouple soil temperature measurements for 1994 at the NSA–OBS site, measured by the Harvard group [open circles; all depths], mid-day measurements on flux observation days by the McGill group [hatched squares; 5, 10, and 20 cm], the U. New Hampshire group [plusses; 10 and 20 cm], and the US Geological Survey group [crosses; 22 cm (on 20 cm plot), and 44 cm (on 50 cm plot); (Winston *et al.* 1995)], and model daily average soil temperatures [lines; all depths]. Model simulation was of several consecutive 1994 weather years (final year reported), so January 1994 followed December 1994 in the model. Snow cover was present (in the model) from Day 305 to Day 136.

the end of the experiment). Water mass for each layer was determined by subtracting the water mass of the adjacent turves (e.g. H layer water mass was determined

by subtracting the LF water mass from the LFH water mass). The sampling design included replicates of each turve set. To roughly match depth increments, model

1994 NSA-OBS Organic Layer Water Contents (g water/g dry matter)
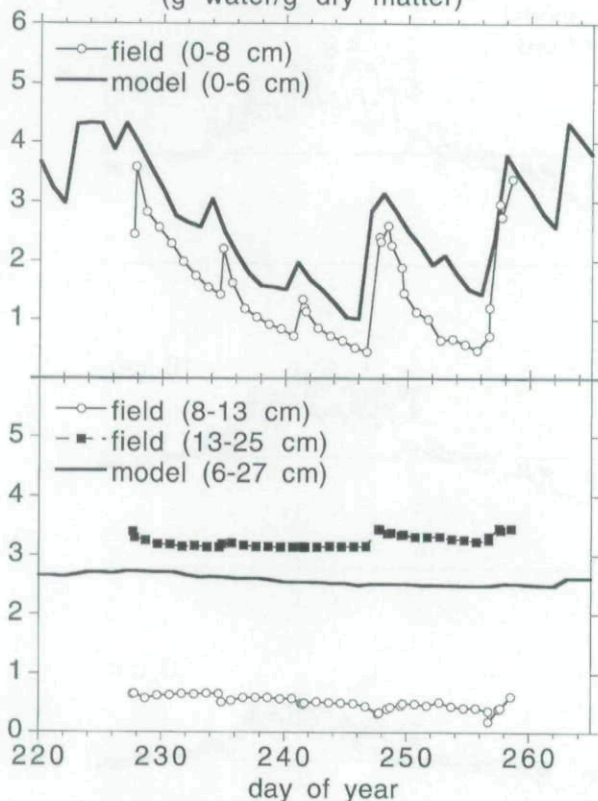
Fig. 4 Water content in the surface organic layers of the soil. Model values (solid lines) are daily averages; gravimetric water content measurements made by the Univ. of Toronto group (solid lines and circles or squares) were twice a day on rainy days, once a day otherwise. See text for brief description of field methodology.

moss (0–3 cm) and litter (3–5.6 cm) layers were averaged and compared with the field L layer (0–8 cm) as weight of water to weight of dry matter (Fig. 4a). The model surface water content tracked the field data, but was slightly wetter. The deeper organic layers (model humus at 5.6–26.7 cm and field 'F' at 8–13 cm and 'H' at 13–20 cm) all had fairly constant water contents over the measurement period (Fig. 4b). The field data indicate that the 'F-layer' (8–13 cm) held much less water than the 'H-layer' (13–25 cm); the model had no corresponding dry band in the organic profile. Both field and model indicate that most of the soil water dynamics occurred in the surface organic layer, while the deeper organic layers and mineral soil (in the model) were generally much more constant.

Ecosystem carbon balance results

Soil dark respiration was compared to opaque, static chamber CO_2 flux measurements (methodology described in Crill 1991) by the USGS group (Winston *et al.* 1995), the UNH group, and the McGill group. Total soil dark respiration was live root respiration plus heterotrophic respiration (litter/peat decay) plus live moss metabolic respiration. Field data were plotted as the average of all reported sites (UNH: $n = 4$; McGill: $n \leq 6$; USGS: $n = 3$–4). Summer season soil respiration observed by the UNH group was much higher than that observed by the McGill group. This was consistent with the much warmer soil temperatures observed at the UNH site (see Fig. 3). Model soil respiration during the warm months was generally consistent with the UNH observations and much higher than the McGill observations (Fig. 5), despite the fact that model soil temperatures were closer to (but warmer than) the McGill observations. Day-to-day variability in the model soil respiration was almost entirely due to wetting and drying cycles in the moss influencing moss metabolic activity. The field sampling scheme may not have been frequent enough to capture this, or the model may have overestimated the variability. Soil respiration (through the snowpack) was non-zero throughout the winter (Fig. 5); model fluxes were higher than observed by the USGS group during the coldest months. Very high spatial variability was observed in spring-time soil respiration (Winston *et al.* 1995).

Net Ecosystem Exchange was compared to daily average eddy correlation net CO2 flux data (methodology described in Fan *et al.* 1995). There was general agreement throughout the year (Fig. 6a,b). The model captured the gradual ecosystem transition from carbon sink to carbon source in the autumn quite well; the spring transition from carbon source to sink appeared to be more rapid, but was not well captured in the field in 1994. During the warm season, the variability in NEE from day to day was generally synchronized between model and field data, but the magnitude of model variability was usually greater (Fig 6b). The model exhibited very high net ecosystem respiration occasionally during the late summer and early fall (NEE > 1.5 g C m^{-2}); these were primarily due to high levels of moss respiration and near neutral carbon balance for the spruce. The model also had high rates of uptake in the early summer (NEE < –3 g C m^{-2}), which occurred on days when both the spruce and the moss net carbon uptake were high. Autumn, early- and late-winter site respiration rates were generally well-captured by the model (there were no data collected at the tower in January and February of 1994) and played a significant role in the site carbon balance. However, model (and actual) NEE is the net result of many processes, and agreement in overall behaviour could mask model errors in individual components, just as disagreement in overall behaviour could mask correct simulation of certain components. A challenge to future

Fig. 5 Model daily average total soil respiration (moss metabolic plus live roots plus heterotrophic) and means of several static, dark chamber measurements made independently by groups from the US Geological Survey (Winston *et al.* 1995), McGill Univ. and the Univ. of New Hampshire (UNH) group. Soil respiration is non-zero throughout the year. In the model summer soil respiration is dominated by the live moss, with much of the modeled variability due to wetting and drying cycles in the live moss. Much higher fluxes for the UNH chambers are probably due, at least in part, to significantly warmer soil temperatures at sites measured by UNH group than at sites measured by McGill group (see Fig. 3).

1994 NSA-OBS Soil Dark Respiration
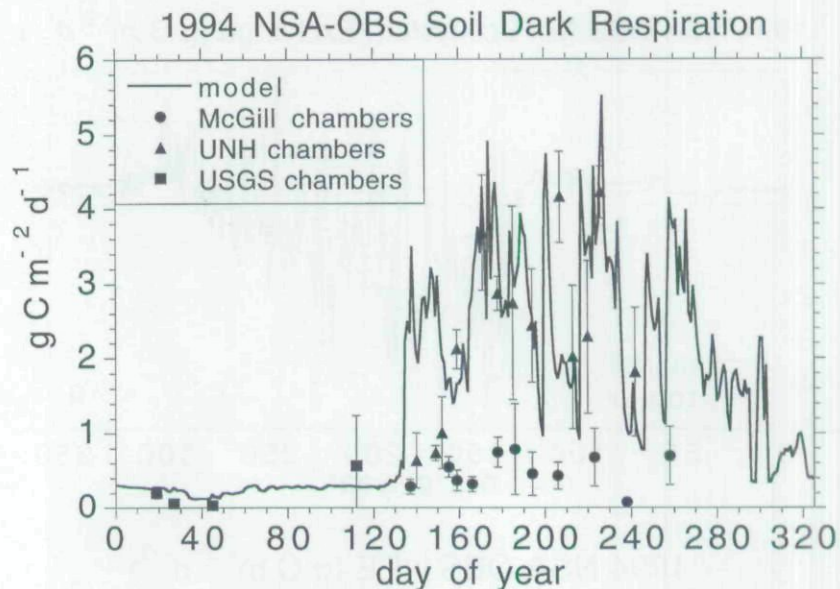
field studies is to try to partition daily NEE into separate components.

Discussion of model validation

Soil respiration rates through the summer (snow-free) season (415 g C m^{-2}) compared closely to those measured in 1980 and 1981 in an Alaskan black spruce/feathermoss forest (367–370 g C m^{-2}) by Schlentner and Van Cleve (1985). Soil dark respiration was the sum of fine root respiration, moss metabolic respiration, and heterotrophic respiration associated with litter decomposition. Measurements for a temperate deciduous forest partitioned soil respiration as roughly 33% live root respiration, 37% from aboveground litter, and 30% from belowground litter (Bowden *et al.* 1993). Such measurements have not been done for sites with bryophyte ground cover, where the situation is very different. In these sites an overlying moss layer is metabolically active (exhaling CO_2), and also serves to insulate the litter, soil, and tree roots from warm summer temperatures (reducing decomposition and root respiration rates). For the NSA–OBS site, the model results suggested that during mid-summer moss metabolic respiration generally accounts for about 50–80% of total soil respiration, roots about 3–14%, and organic matter decomposition (heterotrophic respiration) about 10–40%. However, given that model temperatures were much lower than observed by the UNH group while soil respiration was comparable, and that summer soil respiration was dominated (in the model) by the live moss respiration, it is likely that moss respiration rates for a given temperature were probably too high in the model.

During the warm season, CO_2 production from decom-

position in the litter layer was about twice that of the much thicker, older humus layer, while during the cold season their contributions were more equal, as the litter layer was colder than the humus layer. Only during February did model soil temperatures drop low enough (below –7°C) in the litter layer to stop decomposition. The dry second half of the summer caused several sharp drops in moss respiration, while the deeper litter and roots were subjected to less climatic variability. Root respiration rates (0.001–0.0014 g C g^{-1} fine root C d^{-1} during the summer (at model soil temperatures of 5–10°C) were comparable to rates measured for black spruce seedlings at 5°C and 15°C in laboratory experiments (Conlin & Lieffers 1993).

Both the black spruce and the feathermoss were most productive in the early part of the summer (Fig. 7a,b). Spruce sapwood, root, and foliage respiration were all modeled as simple exponential functions of temperature, and thus all respired even during the coldest months. Feathermoss photosynthesis and respiration were set to zero for moss temperatures below –1°C. Both spruce and moss oscillated rapidly between days of high and low productivity. For the spruce, low productivity days had basically no net exchange of carbon, while for the moss there was a net flux of carbon to the atmosphere on many days. The day-to-day variability for the spruce was primarily due to air temperature variability. For the moss, the days of positive NPP (carbon loss) during the summer corresponded to days of low illumination (often rainy days). This would help explain the spikiness of the moss NPP curve (Fig. 7b), because immediately following a rain the moss was wet and conditions were more ideal for production than after an extended dry spell. Moss respiration began (at very low rates) about 10 days before
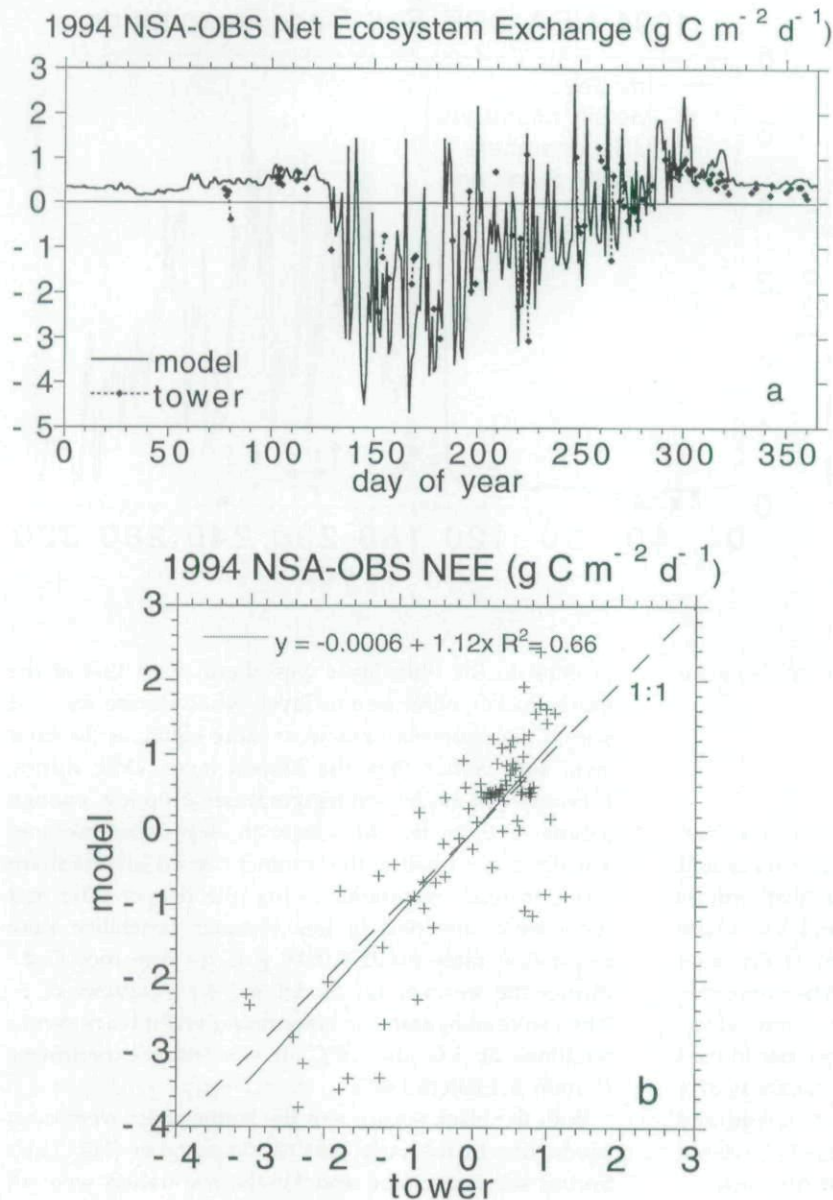
1994 NSA-OBS Net Ecosystem Exchange (g C m⁻² d⁻¹)

$$\text{1994 NSA-OBS Net Ecosystem Exchange (g C m}^{-2}\text{ d}^{-1})$$

1994 NSA-OBS NEE (g C m⁻² d⁻¹)

$$\text{1994 NSA-OBS NEE (g C m}^{-2}\text{ d}^{-1})$$

$y = -0.0006 + 1.12x \ R^2 = 0.66$

Fig. 6 (a) Daily average net ecosystem exchange of carbon as measured at high frequency by an eddy correlation flux tower run by the Harvard group (circles; consecutive days are connected with a dashed line) and simulated by the model (solid line). Positive values represent a net flux from the biosphere to the atmosphere; negative values represent a net flux from the atmosphere to the biosphere. (b) Comparison of daily average NEE for model and tower.

final snowmelt; photosynthesis began two days before final snowmelt (when snow depth dropped to about 3 cm). Spruce had a gradual onset of photosynthesis beginning about 10 days before final snowmelt, when the litter layer thawed sufficiently to make soil water available to the roots. Both NPP curves show a seasonal asymmetry (rapid increase in uptake in early summer, slower decline in uptake in the fall) due in general to the peaking of light intensity early in the summer (relative to air and soil temperatures) and, in this particular year for the moss, to a dry August and September. Total respiration, on the other hand, was more symmetric and with a broad peak in mid-summer, tracking air and soil temperatures.

The model simulation showed a net carbon uptake by

the ecosystem of 51 g C m⁻², or 0.51 t C ha⁻¹, consistent with measured annual NEE. Black spruce NPP was 93 g C m⁻², with 51 g C m⁻² assumed to be lost as above- and below-ground litter. Viereck *et al.* (1983) report mean annual tree productivity for black spruce forests in central Alaska as about 55 g C m⁻². Feathermoss NPP was 58 g C m⁻², comparable to 36–60 g C m⁻² observed in spruce/ moss forests in central Alaska (Oechel & Van Cleve 1986) and Scandinavia (Tamm 1953), as well as estimates for feathermoss productivity in Quebec of 16–60 g C m⁻² (Weetman & Timmer 1967). Total litter inputs to the soil were slightly larger than annual heterotrophic respiration, making the soil a slight carbon sink (8.8 g C m⁻² or 0.088 t C ha⁻¹), while spruce net growth was 42 g C m⁻², or 0.42 t C ha⁻¹. This partitioning of NEE into spruce
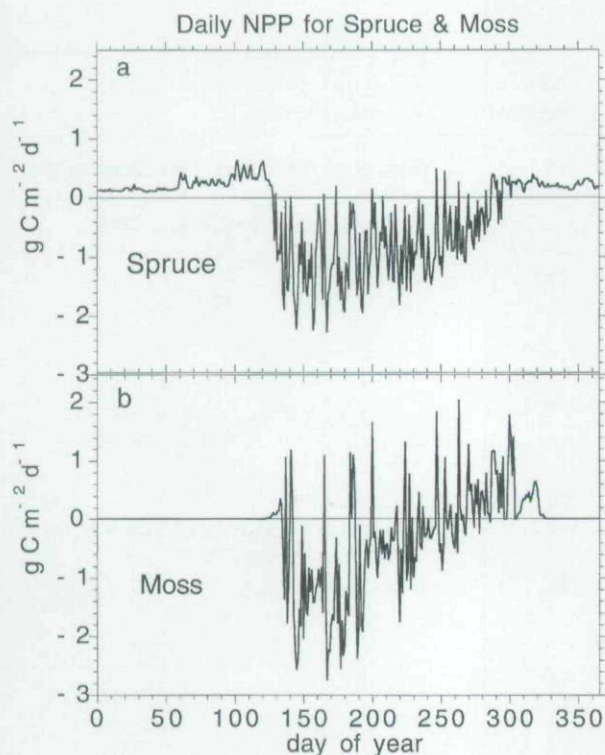
Daily NPP for Spruce & Moss

Fig. 7 Daily NPP of (a) black spruce and (b) feathermoss, as simulated by the model. Positive values represent a net flux from the biosphere to the vegetation; negative values represent a net flux from the atmosphere to the vegetation. NPP was calculated as gross photosynthesis minus total plant respiration. Moss photosynthesis and respiration rates were set to zero for moss temperatures below −1°C. Both spruce and especially moss had asymmetric productivity curves, with higher productivity in early summer, and low productivity in late summer.

growth and soil carbon accumulation depended on a fairly rough characterization of the carbon biomass and dynamics of the black spruce fine roots. Increasing the fine root turnover rate would reduce black spruce productivity, increase heterotrophic respiration somewhat (by increasing the fine root litter pool size), and increase the rate of carbon sequestration into the soil by increasing annual carbon inputs. The net effect would be a small reduction in overall NEE.

Ecosystem respiration in winter plays a significant role in the NEE for a northern ecosystem (e.g. Winston *et al.* 1995; Sommerfeld *et al.* 1993; Wofsy *et al.* 1993). For the NSA-OBS simulation, net carbon uptake during the snow-free season of 1994 (169 days) was 144 g C m^{-2}, while ecosystem respiration during the 1994 snow-cover season (196 days) was 84 g C m^{-2}, 58% of snow-free season uptake. Respiration occurred during every month of the year, indicating that year-round monitoring of the carbon exchange is necessary even in northern ecosystems.

The daily time-step carbon balance model developed by Bonan (1991a), applied to boreal forest ecosystems in interior Alaska, also displayed short-term variability in NEE, low levels (but non-zero) of ecosystem respiration throughout the winter, and an extremely abrupt onset of carbon uptake in the spring. Mid-summer carbon uptake rates simulated for black spruce stands were about three times higher than reported here.

Model sensitivity

A series of 120 model runs were carried out for the 1994 NSA-OBS simulation. In each case a single model parameter was raised or lowered (usually by 20%) from its NSA-OBS simulation value. Few if any of the parameters used were constrained to that degree by the limited published data available. Overall model sensitivity was evaluated by comparing simulated annual NEE for the adjusted parameter runs to the simulated annual NEE for the standard run (51.1 g C m^{-2}). Tables 1–3 and 5 contain a summary of the sensitivity results; values reported are the average magnitude change in total annual ecosystem NEE (as a percentage of the standard run) for the two sensitivity runs for each parameter.

Ecosystem NEE was quite sensitive to the initial carbon pool sizes of foliage, sapwood, fine roots, and the surface organic layer (moss plus peat) (Table 1). Increasing moss bulk density (Table 2) reduced moss productivity by causing a greater light extinction rate in the moss and thus effectively adding poorly illuminated, respiring live tissue. It also reduced heterotrophic respiration, probably because of reduced moss litter inputs into the decomposition pool. Because moss water contents were calculated on a per mass basis, increased bulk density increased moss water holding capacity, which dried out the deeper soil (1994 was a dry year) and thus reduced spruce productivity as well.

Some of the very high sensitivities observed were the result of ecosystem NEE being much less than gross ecosystem photosynthesis and gross ecosystem respiration. For example, a 20% increase in spruce maximum photosynthetic rate increased site NEE by about 66%, because site NEE was only about 16% of spruce gross photosynthesis for 1994 (the change in spruce NPP was 35%, again reflecting the fact that NPP is smaller than gross photosynthesis). Thus a change in the rate of photosynthesis produced a magnified change in site NEE. This effect points to a potential sensitivity of any ecosystem where the net carbon exchange is only a small fraction of the gross fluxes of carbon into and out of the ecosystem. Any change or disturbance that predominantly effects only one component of the carbon balance could have a large impact on overall ecosystem NEE.

Ecosystem NEE was also quite sensitive to many of the parameters associated with the respiration calculations; again annual NEE was only about half of annual hetero-

Table 5 Model parameters— decomposition

Parameter	Value	Units	Description	NEE Sensitivity[1]	Reference/Source
R_o	0.15	y^{-1}	mean annual mass loss rate	18	Berg *et al.* 1993; Berg 1984, Ivask *et al* 1991
Δ_{fr}	0.25	y^{-1}	fine root turnover rate	1	Arthur & Fahey, 1992; Fogel, 1983
α	1.0		mass loss rate parameter	– –	Heal *et al.* 1978
$(dm/dt)_{h-o}$	1/40		humus/fresh litter mass loss rate	13	–

Temperature

$$f(T) = \begin{cases} 0 & \text{if } T < T_{min} \\ (Q_{10})^{-T_{base}/10}((T - T_{min})/|T_{min}|)^{0.5} & \text{if } T_{min} \leq T \leq 0°C \\ (Q_{10})^{(-T_{base})/10} & \text{if } T > 0°C \end{cases}$$

$Q_{10,r}$	2.0		exponential response - temp	20	Hogg *et al* 1992
T_{min}	–7.0	°C	minimum temperature	4	Flanagan & Veum 1974; Clein & Schimel 1995; Winston et *al* 1995
T_{base}	10	°C	reference temperature	21	Hogg *et al* 1992

Moisture

$$f(T) = \begin{cases} 0 & \text{if } W < W_{min} \\ (W - W_{min})/(W^* - W_{min}) & \text{if } W_{min} \leq W \leq W^* \\ 1 & \text{if } W^* \leq W \leq W_{fc} \\ 1 - (W - W_{fc})/[2(1 - W_{fc})] & \text{if } W > W_{fc} \end{cases}$$

Litter layer

W_{min}	0.25	g water g^{-1} dry	minimum water content	0	Reynolds & Knight, 1973
W^*	1.0	g water g^{-1} dry	moderate water content	1	–
W_{fc}	3.0	g water g^{-1} dry	field capacity	1	Reynolds & Knight, 1973

Humus layer

W_{min}	0.25	g water g^{-1} dry wt	humus min. water content	0	Reynolds & Knight, 1973
W^*	2.0	g water g^{-1} dry wt	humus moderate water	16	–
W_{fc}	3.0	g water g^{-1} dry wt	humus field capacity	31	Reynolds & Knight, 1973

1, Parameters raised and lowered 20%. Value is average magnitude of change (%) in total ecosystem NEE for the two sensitivity runs.

trophic respiration and less than half of moss or spruce foliar respiration, so effects were magnified in these cases. However, because the organic and mineral soils are generally quite cool (often cooler than the base temperature used for the temperature dependency on decomposition), increasing Q_{10} values had the effect of reducing respiration losses. A higher Q_{10} causes respiration to rise more quickly above the base temperature, but it also causes respiration rates to drop more quickly below the base temperature.

Moss productivity was very sensitive to parameters controlling both its light environment (moss bulk density and light extinction rates in the spruce and moss canopies) and its response to light (moss half-saturation constant).

Because the model calculated light extinction in the moss canopy and moss productivity at 10 levels of illumination down the canopy, model moss productivity was very sensitive to photosynthesis rates at low light. Changing the half-saturation illumination constant for the moss from 40 to 48 µE PAR m^{-2} s^{-1} reduced moss productivity by over 50%. This is a crucial sensitivity that will require more field data to reduce model uncertainty.

Model application— interannual variability

The model was used to simulate NSA–OBS carbon balance for October 1967 through December 1989, using AES daily meteorological data (T_{max}, T_{min}, precipitation)
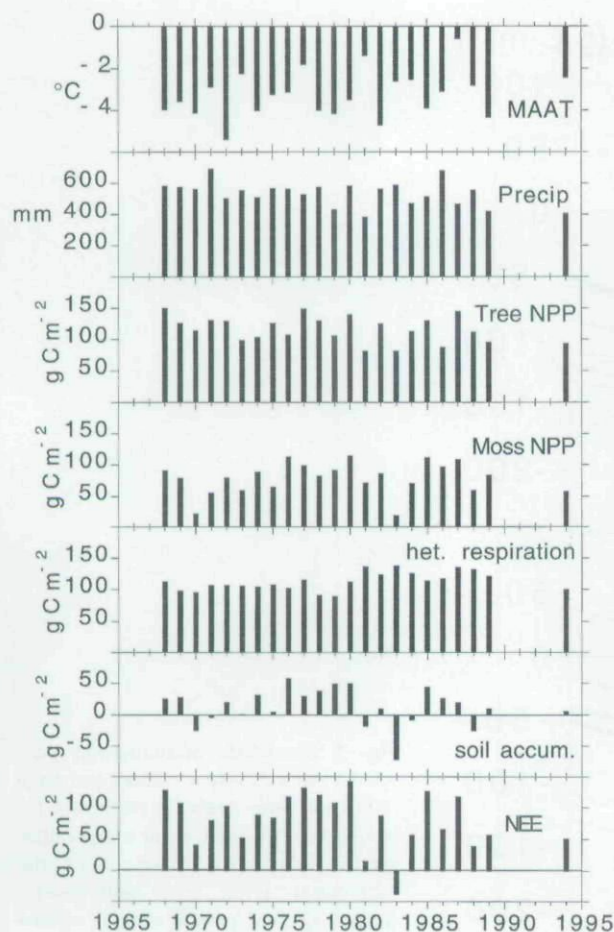
Fig. 8 Interannual variability (1968–1989 and 1994) of (a) mean annual air temperature; (b) total annual precipitation; (c) model simulated annual spruce net primary productivity (NPP); (d) model simulated annual feathermoss NPP; (e) model simulated annual heterotrophic respiration (decomposition); (f) model simulated annual soil carbon accumulation (equals litterfall minus heterotrophic respiration); and (g) model simulated annual net ecosystem carbon exchange (NEE).

from the Thompson Airport. PAR input values were generated with (2). Site initialization was identical to the 1994 run presented above. Results for each year were compared with 1994 model results to get an idea of how representative 1994 may have been (an important issue for a major field campaign), and also to begin to examine what factors most strongly influence interannual variability in carbon balance.

Weather variability

Long-term mean annual air temperature for Thompson is about –3.9°C. For 1968–1989 and 1994 mean annual air temperature ranged from –0.6°C in 1987 to –4.7°C in 1982 (Fig. 8a). For 1994, air temperature was cold

in January and February, cool to normal for March through October, and warmer than normal in November and December. The timing of the annually accumulating, degree day minimum (i.e. the timing of the onset of spring thaw) varied considerably, from as early as Day 98 (1984) to as late as Day 139 (1983). The timing of the degree day maximum (fall freeze) was less variable, ranging from Day 289 (1981 and 1982) to Day 310 (1983). Long-term mean annual precipitation for Thompson is about 534 mm, with about 60% as rain; 1968–1989 precipitation ranged from 383 mm in 1981– 692 mm in 1971 (Fig. 8b). Precipitation in 1994 was abundant in February, March, and June, and quite low for July through October.

Carbon balance

Average, simulated black spruce NPP for the 1968–1989 and 1994 was 116 g C m^{-2} y^{-1}, with a range from 81 to 150 g C m^{-2} y^{-1} (Fig. 8c). Average feathermoss NPP for this period was 78 g C m^{-2} y^{-1}, with a range from 19 to 114 g C m^{-2} y^{-1} (Fig. 8d). Interannual variability in productivity in the feathermoss was similar in timing but greater in relative magnitude to that for the black spruce. For both, 1994 productivity was slightly below the 1968–89 mean. High productivity years were characterized by early spring (1977 and 1987), cool summer (1985), and, for mosses, abundant summer precipitation (1976, 1980 and 1985). Low productivity years (1981, 1983 and 1986 for spruce; 1970 and 1983 for moss) were characterized by late springs (in 1983 model snowmelt was three weeks later than any other year) and infrequent and below-average precipitation (1981). In 1970, an early heavy snowfall buried the moss before it could freeze, so it had significant respiration losses in the fall (75% of summer NPP). Moss productivity was near normal in 1981 despite low precipitation. The model simulated high moss productivity rates in May and June of 1981 following snowmelt, and because there were a number of small storms during June that would have been sufficient to wet the moss.

Average heterotrophic respiration for the 1968–89 and 1994 was 113 g C m^{-2} y^{-1} and all years were within about 20% of this value (Fig. 8e). This relatively low interannual variability was due to two factors. First, by model design spruce litter inputs were identical each year (independent of plant productivity); moss litter fall varied from year to year (based on moss productivity). Thus fresh litter input variability was probably underestimated. Secondly, decomposition occurred in the litter, humus, and upper mineral soil layers, where it was buffered from the weather variability by the overlying moss. The lowest value for heterotrophic respiration was 89 g C m^{-2} y^{-1} in 1979, one of the cooler years of the period; heterotrophic
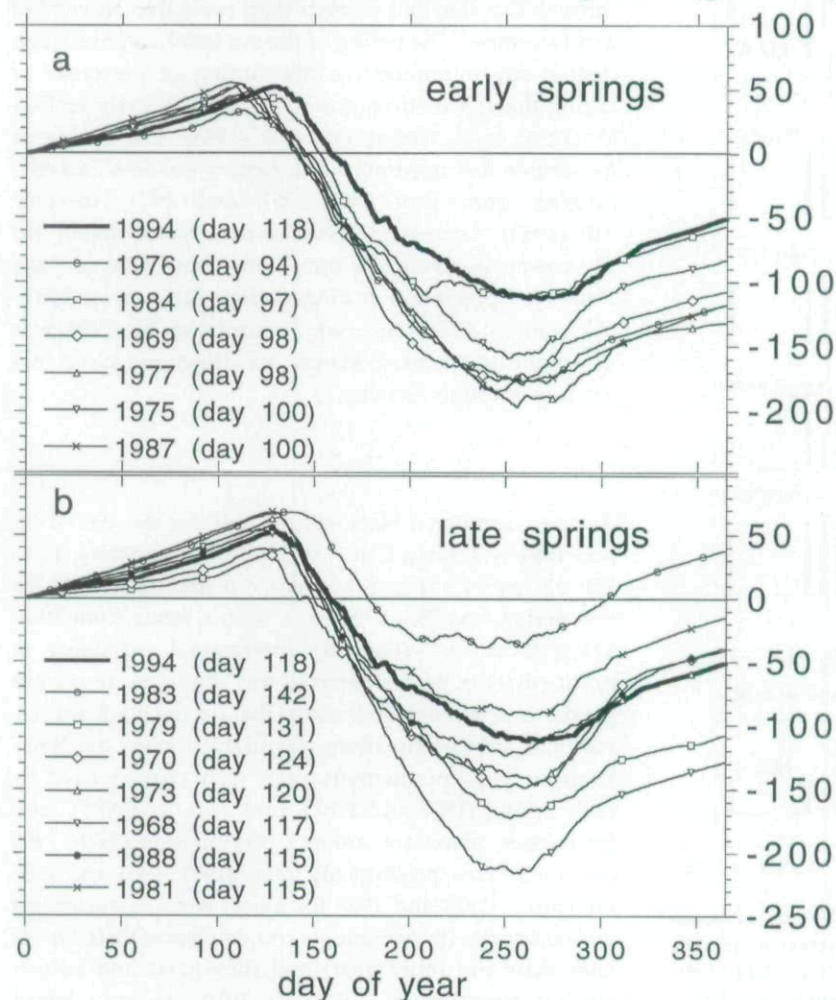
NSA-OBS Spruce/Moss Accumulating NEE (g C m⁻²)

Fig. 9 Simulated, accumulating ecosystem net ecosystem carbon exchange (NEE) for years with (a) early and (b) late springs (defined as air temperature greater than zero for most of the subsequent days). Years with 'early' springs all had greater carbon uptake than 1994; years with 'late' springs were more variable, but averaged a lower NEE than 1994. Other climatic factors play a role in interannual variability of NEE (see text for a more complete discussion).

respiration in 1994 (100 g C m⁻²) was also below average, probably because of fairly cool temperatures and a dry second half of the year. Soil carbon accumulation is the net effect of litterfall and heterotrophic respiration. The 1968–89 and 1994 average was 13 g C m⁻², with high variability and several years showing a net loss of carbon from the soil (Fig. 8f). This result was very dependent on a simple (and poorly constrained) representation of black spruce fine root dynamics.

The simulated net annual carbon uptake by the black spruce/feathermoss forest ranged from –37 g C m⁻² (loss of 0.37 t C ha⁻¹) to 142 g C m⁻² (1.42 t C ha⁻¹); 1994 NEE (51 g C m⁻²) was below the 1968–1989 mean of 82 g C m⁻² (Fig. 8g). Lowest NEE years combined low productivity with high heterotrophic respiration. High NEE correlated with high plant productivity.

Discussion of interannual variability

The ranges of simulated values for black spruce and moss productivity are in accord with measurements in Alaska (e.g. Van Cleve *et al.* 1983; Viereck *et al.* 1983; Oechel & Van Cleve 1986) and Canada (Weetman & Timmer 1967; DeAngelis *et al.* 1981). Interannual variability in the model was driven primarily by variability in weather from one year to the next. In a nine year simulation (1974–1982) of 23 boreal forest stands near Fairbanks, AK (9 black spruce, 5 white spruce, 3 poplar, 2 birch, 2 aspen, and 2 mixed conifer), using a similar model also driven by observed daily weather, Bonan (1992) reported a trend in the seasonal amplitude of CO_2 flux (amplitude equals maximum daily NEE minus minimum daily NEE simulated each year), but little interannual variability in tree NPP, moss NPP, or ecosystem NEE. These results were reported as averages of the 23 ecosystems and may have masked interannual variability at a single site.

Lieth (1975) developed regressions relating mean annual biotemperature (sum of all daily air temperatures greater than 0°C divided by 365) and total annual precipitation to NEE across a range of terrestrial ecosystems,

with productivity tending to increase with each factor. Dai & Fung (1993) extended this model to look at interannual variability in NEE driven by interannual variability in mean annual temperature and total annual precipitation. Kojima (1994) also used Lieth's productivity algorithms to evaluate the potential impact of climate warming on productivity in boreal ecosystems. In the simulations reported here, however, this simple relationship of higher NEE with higher biotemperature and/or precipitation did not hold true. For example, the least productive year (1983) had an above-normal annual biotemperature and slightly above-normal annual precipitation. It also had an extremely late spring, and a fairly dry May and June. A closer look at the weather patterns through the year (e.g. timing of snowmelt and snowfall, frequency and timing of summer storms, summer heat waves) was required to explain interannual variability.

One factor that appeared to play a strong role in influencing interannual variability of the spruce/moss forest NEE was the timing of spring. Because both the moss and spruce are evergreen, they can begin photosynthesis as soon as conditions are favorable. Spring comes late in the northern boreal forest, so that, by the time the snow has melted, light levels are high and the air is usually warming rapidly. The simulated onset of moss respiration and net positive photosynthesis indicated a variability of as much as 5 weeks in the onset of physiological spring, and the most (least) productive years tend to be those with the earliest (latest) transition to net carbon uptake (Fig. 9). For the moss the controlling factor appeared to be loss of snow cover, for the spruce it was the closely linked factor of the thawing of the soil and availability of water. This is likely to be a major factor in any impact of climate change, and may also account for much of the interannual variability that would be observed in multi-year studies.

Conclusions

The impact of weather/climate variability on the carbon balance of a spruce/moss boreal forest was investigated with a new daily time-step model of litter decomposition and tree and moss photosynthesis and respiration. The model simulated carbon balance compared well with preliminary data collected in the 1994 BOREAS campaign in northern Manitoba, and with other reported values. Model analyses showed the spruce/moss ecosystem to be a carbon sink, with a strength of 51.1 g C m^{-2} in 1994. Winter respiration fluxes were significant, with a simulated flux of 83.6 g C m^{-2} to the atmosphere while the ground was snow-covered (1 November to 15 May). Simulated NEE for 1968 through 1989 averaged −82 g C m^{-2} (uptake of 0.82 t C ha^{-1} y^{-1}), with a range of +37 and −142 g C m^{-2}. Moss and spruce NPP generally

varied together, both tending to be high in years with early springs and relatively wet summers, and both low in years with late springs and relatively dry summers. Heterotrophic respiration was more constant in all years simulated (mean = 113 g C m^{-2}). The sensitivity of ecosystem productivity to the timing of spring occurred both because of the high light levels present by mid–late spring (early May potential irradiance equals mid-August potential irradiance), and because of generally abundant water soon after snowmelt. The timing of fall snow and freeze up appeared to have much less impact on productivity, although an early, deep snow in 1970 may have enhanced autumn respiration. If spring thaw tends to get earlier in the year due to any climatic change, it is likely that either these ecosystems will become more productive or enhanced spring productivity will offset at least some productivity losses that may be caused by other changes. Sustained higher productivity would depend on sufficient nutrient availability, which has not been addressed in this modeling study. Changes or variability in annual climatological variables such as annual biotemperature and total annual precipitation are not likely to be effective indicators of the change or variability in the boreal spruce/moss ecosystem's carbon balance.

Acknowledgements

References

Aber JD, Federer CA (1992) A generalized, lumped parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia*, **92**, 463–474.

Aber JD, Reich PB, Goulden ML (1996) Extrapolating leaf CO2 exchange to the canopy: a generalized model of forest photosynthesis validated by eddy correlation. *Oecologia* (in press).

Arthur MAT, Fahey J (1992) Biomass and nutrients in an Engelmann spruce-subalpine fir forest in north central Colorado: pools, annual production, and internal cycling. *Canadian Journal of Forest Research*, **22**, 315–325.

Barney RJ, Van Cleve K (1973) Black spruce fuel weights and biomass in two Interior Alaska stands. *Canadian Journal of Forest Research*, **3**, 304–311.

Berg B (1984) Decomposition of moss litter in a mature Scots pine forest. *Pedobiologia*, **26**, 301–308.

Berg B, Ekbohm G (1991) Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. *Canadian Journal of Botany*, **69**, 1449–1456.

Berg B, Berg MP, Bottner P, and 15 others (1993) Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry*, **20**, 127–159.

Billings WD (1987) Carbon balance of Alaskan tundra and taiga ecosystems: past, present, and future. *Quaternary Science Review*, **6**, 165–177.

Boelter DH, Verry ES (1978) *Peatland and Water in the Northern Lake States*. USDA Forest Service General Technical Report NC-31, North Central Forest Experiment Station, Grand Rapids MN, 22 pp.

Bonan GB (1993) Physiological controls of the carbon balance of boreal forest ecosystems. *Canadian Journal of Forest Research*, **23**, 1453–1471.

Bonan GB (1992) Comparison of atmospheric carbon dioxide concentration and metabolic activity in boreal forest ecosystems. *Tellus*, **44B**, 173–185.

Bonan GB (1991a) Atmosphere-biosphere exchange of carbon dioxide in boreal forests. *Journal of Geophysical Research*, **96**, 7301–7312.

Bonan GB (1991b) A biophysical surface energy budget analysis of soil temperature in the boreal forests of interior Alaska. *Water Resources Research*, **27**, 767–781.

Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM, Garrison JB (1993) Contributions of aboveground litter, belowground litter, and root respiration in total soil respiration in a temperate mixed hardwood forest. *Canadian Journal of Forest Research*, **23**, 1402–1407.

Bunnell FL, Tait DEN, Flanagan PW (1977) Microbial respiration and substrate weight loss. II. A model of the influences of chemical composition. *Soil Biology and Biochemistry*, **9**, 41–47.

Busby JR, Whitfield DWA (1978) Water potential, water content, and net assimilation of some boreal forest mosses. *Canadian Journal of Botany*, **56**, 1551–1558.

Busby JR, Bliss LC, Hamilton CD (1978) Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecological Monographs*, **48**, 95–110.

Campbell GS (1985) *Soil Physics with Basic*. Elsevier, Amsterdam, 150 pp.

Ciais P, Tans PP, Trolier M, White JWC, Francey RJ (1995) A large northern hemisphere terrestrial CO_2 sink indicated by the $^{13}C/^{12}C$ ratio of atmospheric CO_2. *Science*, **269**, 1089–1102.

Clein JS, Schimel JP (1995) Microbial activity of tundra and taiga soils at sub-zero temperatures. *Soil Biology and Biochemistry*, **27**, 1231–1234.

Conlin TSS, Lieffers VJ (1993) Anaerobic and aerobic CO2 efflux rates from boreal forest conifer roots at low temperatures. *Canadian Journal of Forest Research*, **23**, 767–771.

Crill P (1991) Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochemical Cycles*, **5**, 319–334.

Dai A, Fung IY (1993) Can climate variability contribute to the 'missing' CO2 sink? *Global Biogeochemical Cycles*, **7**, 599–610.

DeAngelis DL, Gardner RH, Shugart HH (1981) Productivity of forest ecosystems studied during the IBP: the woodlands data set. In: *Dynamic Properties of Forest Ecosystems* (ed. Reichle DE). Cambridge University Press, Cambridge.

Denning AS, Fung IY, Randall D (1995) Latitudinal gradient of atmospheric CO2 due to seasonal exchange with land biota. *Nature*, **376**, 240–243.

Dilks TJK, Proctor MCF (1979) Photosynthesis, respiration and water content in bryophytes. *New Phytologist*, **82**, 97–114.

Dingman SL (1994) *Physical Hydrology*. Macmillan, New York, 575 pp.

Dunne T, Leopold L (1978) *Water in Environmental Planning*. WH Freeman, NY, 818 pp.

Dyrness CT, Grigal DF (1979) Vegetation-soil relationships along a spruce transect in interior Alaska. *Canadian Journal of Botany*, **57**, 2644–2656.

Enting IG, Mansbridge JV (1991) Latitudinal distribution of sources and sinks of CO2: results of an inversion study. *Tellus*, **43B**, 156–170.

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

Federer CA (1995) *BROOK90: A simulation model for evapotranspiration, soil water, and streamflow*, version 2.1 (computer freeware and documentation), USDA Forest Service, PO Box 640, Durham NH 03824 USA.

Flanagan PW, Veum AK (1974) Relationships between respiration, weight loss, temperature, and moisture in organic residues on tundra, In: *Soil Organisms and Decomposition in Tundra* (eds Holding AJ, Heal OW, MacLean SW, Flanagan PW), pp. 249–278. IBP Tundra Biome Steering Committee, Stockholm.

Flyes JW, McGill WB (1987) Decomposition of boreal forest litters from central Alberta under laboratory conditions. *Canadian Journal of Forest Research*, **17**, 109–114.

Fogel R (1983) Root turnover and productivity of coniferous forests. *Plant and Soil*, **71**, 75–85.

Frolking S, Crill P (1994) Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: measurement and modeling. *Global Biogeochemical Cycles*, **8**, 385–397.

Golding DL., Stanton CR (1972) Water storage in the forest floor of subalpine forests of Alberta. *Canadian Journal of Forest Research*, **2**, 1–6.

Green TGA, Lange OL (1994) Photosynthesis in poikilohydric plants: a comparison of lichens and bryophytes. In: *Ecophysiology of Photosynthesis* (eds Schulze E-D, Caldwell MM), pp. 319–341. Springer-Verlag, Berlin.

Heal OW, Latter PM, Howson G (1978) A study of the rates of decomposition of organic matter. In: *Production Ecology of British Moors and Montane Grasslands* (eds Heal OW, Perkins DF), pp. 136–159. Springer-Verlag, Berlin.

Hendricks JJ (1994) *Assessing the effects of nitrogen availability on fine root turnover and tissue chemistry in forest ecosystems,* PhD Dissertation, University of New Hampshire, Durham NH.

Hogg EH, Lieffers VJ, Wein RW (1992) Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire. *Ecological Applications,* **2,** 298–306.

Hogg EH (1993) Decay potentials of hummock and hollow Sphagnum peats at different depths in a Swedish raised bog. *Oikos,* **66,** 269–278.

Hom JL Oechel WC (1983) The photosynthetic capacity, nutrient content, and nutrient use efficiency of different needle age-classes of black spruce (Picea mariana) found in interior Alaska. *Canadian Journal of Forest Research,* **13,** 834–839.

Hunt ER, Running SW (1992) Simulated dry matter yields for aspen and spruce stands in the North American boreal forest. *Canadian Journal of Remote Sensing,* **18,** 126–133.

Ivask M, Lohmus K, Rasta E (1991) Below-ground tree productivity of a norway spruce forest: a preliminary report, In: *Plant Roots and Their Environment* (eds McMichael BL, Persson H), pp. 213–217. Elsevier, Amsterdam.

Kojima S (1994) Effects of global climate warming on the boreal forest. *Journal of Plant Research,* **107,** 91–97.

Larsen JA (1980) *The Boreal Ecosystem.* New York, Academic Press 500 pp.

Lieth H (1975) Modeling the primary productivity of the world. In: *Primary Productivity of the Biosphere* (eds Lieth H, Whittaker RH), pp. 237–263. Springer-Verlag, New York.

Longton RE (1988) *The Biology of Polar Bryophytes and Lichens.* Cambridge, UK: Cambridge Univ. Press, 391 pp.

Lüdeke MKB, Dönges S, Otto RD, Kindermann J, Badeck, F-W, Ramge P, Jägel U, Kohlmaier GH (1995) Responses in npp and carbon stores of the Northern biomes to a CO2-induced climatic change, as evaluated by the Frankfurt Biosphere Model (FBM). *Tellus,* **47,** 191–205.

Lunardini VJ (1981) *Heat Transfer in Cold Climates.* Van Nostrand Reinhold, New York, 731 pp.

Moore TR (1984) Litter decomposition in a subarctic spruce-lichen woodland, Eastern Canada. *Ecology,* **65,** 299–308.

Oechel WC, Billings WD (1992) Effects of global change on the carbon balance of Arctic plants and ecosystems. In: *Arctic Ecosystems in a Changing Climate: An Ecological Perspective* (eds Chapin FS, Jeffries RL, Reynolds JF, Shaver GR, Svoboda J), pp. 139–168. Academic Press, San Diego.

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G, Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature,* **361,** 520–523.

Oechel WC, Van Cleve K (1986) The role of bryophytes in nutrient cycling in the taiga. In: *Forest Ecosystems in the Alaskan Taiga* (eds Van Cleve K, Chapin FS, Flanagan PW, Viereck LA, Dyrness CT), pp. 121–137. Springer-Verlag, New York.

Pritchett WL, Fisher RF (1987) *Properties and Management of Forest Soils.* John Wiley & Sons, New York, 494 pp.

Proctor MCF (1982) Physiological ecology: water relations, light and temperature responses, carbon balance. In: *Bryophyte Ecology* (ed. Smith AJE), pp. 333–382. Chapman and Hall, London.

Reynolds JF, Knight DH (1973) The magnitude of snowmelt and rainfall interception by litter in lodgepole pine and spruce-fir forests in Wyoming. *Northwest Science,* **47,** 50–60.

Running SW, Coughlan JC (1988) A general model of forest ecosystem processes for regional applications. 1. hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling,* **42,** 125–154.

Ryan MG (1991) Effects of climate change on plant respiration. *Ecological Applications,* **1,** 157–167.

Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholz LH, Cropper WP, Running SW (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia,* **101,** 133–140.

Schlentner RE, Van Cleve K (1985) Relationships between CO2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in Alaska. *Canadian Journal of Forest Research,* **15,** 97–106.

Seigenthaler U, Sarmiento JL (1993) Atmospheric carbon dioxide and the ocean. *Nature,* **365,** 119–125.

Sellers P, Hall FG, Margolis H, and 10 others (1995) The Boreal Ecosystem-Atmosphere Study (BOREAS): an overview of early results from the 1994 field year. *Bulletin of the American Meteorological Society,* **76,** 1549–1577.

Sellers P (Chair) and BOREAS Science Steering Committee (1991) Charting the boreal forest's role in global climate change. *EOS,* **72,** 33–40.

Skre O, Oechel WC (1981) Moss functioning in different taiga ecosystems in interior Alaska: 1. seasonal, phenotypic, and drought effects on photosynthesis and response patterns. *Oecologia,* **48,** 50–59.

Skre O, Oechel WC, Miller PM (1983) Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. *Canadian Journal of Forest Research,* **13,** 869–868.

Sommerfeld RA, Mosier AR, Musselman RC (1994) CO2, CH4, and N2O flux through a Wyoming snowpack and implications for global budgets. *Nature,* **361,** 140–142.

Sparrow SD, Sparrow EB, Cochran VL (1992) Decomposition in forest and fallow subarctic soils. *Biology and Fertility of Soils,* **14,** 253–259.

Swift MJ, Heal OW, Anderson JM (1979) *Decomposition in Terrestrial Ecosystems.* Univ. California Press, Berkeley, CA, 372 pp.

Tamm CO (1953) Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). *Medd. fran Stat. Skogsforsknings,* **43,** 1–140.

Tans PP, Fung IY, Takahashi T (1990) Observational constraints of the global atmospheric CO2 budget. *Science,* **247,** 1431–1438.

Tryon PR, Chapin FS (1983) Temperature control over root growth and root biomass in taiga forest trees. *Canadian Journal of Forest Research,* **13,** 827–833.

Van Cleve K, Yarie J (1986) Interaction of temperature, moisture, and soil chemistry in controlling nutrient cycling and ecosystem development in the taiga of Alaska. In: *Forest*

Ecosystems in the Alaskan Taiga (eds Van Cleve K, Chapin FS, Flanagan PW, Viereck LA, Dyrness CT), pp. 160–189. Springer-Verlag, New York.

Van Cleve K, Oliver L, Schlentner R, Viereck LA, Dyrness CT (1983) Productivity and nutrient cycling in taiga forest ecosystems. *Canadian Journal of Forest Research*, **13**, 747–766.

Viereck LA, Dyrness CT, Van Cleve K, Foote MJ (1983) Vegetation, soils, and forest productivity in selected forest types in interior Alaska. *Canadian Journal of Forest Research*, **13**, 703–720.

Waring RH, Schlesinger WE (1985) *Forest Ecosystems: Concepts and Management*. Academic Press, San Diego, 340 pp.

Weetman GF, Timmer V (1967) Feather moss growth and nutrient content under upland black spruce. (Technical Report No. 503) Pulp and Paper Research Institute of Canada.

Winston GC, Stephens BB, Sundquist ET, Hardy JP, Davis RE (1995) Seasonal variability in CO2 transport through snow in a boreal forest. In: *Biogeochemistry of Seasonally Snow-Covered Catchments* (eds Tonnesson KA, Williams MW, Tranter M), pp. 61–70. IAHS Press, Publ. no 228, Wallingford UK.

Wofsy SC, Goulden ML, Munger JW, Fan S-M, Bakwin PS, Daube BC, Bassow SL, Bazzaz FA (1993) Net exchange of CO2 in a mid-latitude forest. *Science*, **260**, 1314–1317.