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Sensitivity of spruce/moss boreal forest net ecosystem productivity to seasonal anomalies in weather

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Abstract. A process-oriented, daily time step model of a spruce/moss boreal ecosystem simulated 1994 and 1995 productivity for a Boreal Ecosystem-Atmosphere Study site near Thompson, Manitoba. Simulated black spruce net primary productivity (NPP) was 139 g C m^{-2} in 1994 and 112 in 1995; feathermoss NPP was 13.0 g C m^{-2} in 1994 and 9.7 in 1995; decomposition was 126 g C m^{-2} in 1994 and 130 in 1995; net ecosystem productivity (NEP) was an uptake of 26.3 g C m^{-2} in 1994 and 2.5 in 1995. A very dry period for the first half of the 1995 summer was the major cause of that year's lower productivity. Sensitivity simulations explored the impact of 2-month long warmer, cooler, wetter, and drier spells on ecosystem productivity. Warmer summers decreased spruce NPP, moss NPP, and NEP; cooler summers had the opposite effect. Earlier snowmelt (due to either warmer spring temperatures or reduced winter precipitation) increased moss and spruce NPP; later snowmelt had the opposite effect. The largest effect on decomposition was a 5% reduction due to a drier summer. One-month droughts (April through October) were also imposed on 1975 base year weather. Early summer droughts reduced moss annual NPP by ~30–40%; summer droughts reduced spruce annual NPP by 10%; late summer droughts increased moss NPP by about 20% due to reduced respiration; May to September monthly droughts reduced heterotrophic respiration by about 10%. Variability in NEP was up to roughly ±35%. Finally, 1975 growing season precipitation was redistributed into frequent, small rainstorms and infrequent, large rainstorms. These changes had no effect on spruce NPP. Frequent rainstorms increased decomposition by a few percent, moss NPP by 50%, and NEP by 20%. Infrequent rainstorms decreased decomposition by 5%, moss NPP by 50% and NEP by 15%. The impact of anomalous weather patterns on productivity of this ecosystem depended on their timing during the year. Multiyear data sets are necessary to understand this behavior and test these types of models.

Introduction

Analysis of the carbon budget of the atmosphere cannot balance carbon sources to the atmosphere (fossil fuel use, land use/land cover change, ecosystem disturbance, ecosystem respiration), carbon sinks (aggrading terrestrial ecosystems, biological and physicochemical oceanic uptake, ecosystem photosynthesis), and changes in the CO_2 concentration of the atmosphere [e.g., *Siegenthaler and Sarmiento*, 1993]. Several analyses that incorporate some spatial resolution point to a carbon sink in the northern temperate/boreal terrestrial biomes (roughly 30°–60°N) [e.g., *Tans et al.*, 1990; *Denning et al.*, 1995; *Ciais et al.*, 1995]. The analysis of *Ciais et al.* [1995] suggests that the magnitude of the terrestrial sink is variable from year to year [see also *Francey et al.*, 1995; *Keeling et al.*, 1995].

Net uptake of carbon by terrestrial ecosystems (i.e., a terrestrial carbon sink) occurs when net primary production (NPP) by vegetation (photosynthesis minus plant respiration) exceeds decomposition of nonliving organic matter (heterotrophic respiration) and other exports. Relationships between NPP and mean annual climatic factors (e.g., annual total precipitation, mean annual biotemperature) have been reasonably

successful at predicting annual NPP for a broad range of ecosystems in different climate zones [e.g., *Leith*, 1975]. Similarly, soil respiration, which includes both heterotrophic respiration and live root or underground biomass respiration, has been shown to correlate with annual temperature and precipitation [*Raich and Schlesinger*, 1992].

Dai and Fung [1993] combined these empirical relationships between mean annual climatology and NPP and soil respiration with historical records of climate variability to demonstrate that interannual climate variability may contribute to interannual variability in the net carbon uptake (or loss) by terrestrial ecosystems over the short term. Their analysis, which provided both temporal and spatial resolution to the net anomalous carbon fluxes between terrestrial ecosystems and the atmosphere, also indicated that temperate/boreal regions were carbon sinks for much of the time from 1955 to 1985 (compared to an assumed zero net carbon exchange for 1920–1949). Globally, the anomalous carbon balance proposed by *Dai and Fung* [1993] was comparable in magnitude to the "missing sink" needed to balance the atmospheric carbon budget. However, the analysis of *Dai and Fung* [1993] made the assumption that the functional relationships between both NPP and soil respiration and annual climatic variables are the same for variability in temperature and/or precipitation at a single site from year to year as for variation in temperature and/or precipitation between climatic zones. These functional

relationships would predict that the NEP of a temperate deciduous forest in the eastern United States during an anomalously hot, dry summer would be the same as NEP for a Mediterranean ecosystem where hot, dry summers are normal; and they would predict that for any ecosystem, a year with a wet winter/dry summer and a year with a dry winter/wet summer (both with the same annual precipitation and temperature) would have the same annual NEP. It is not clear that this would always be the case.

Five years of nearly continuous NEP measurements by the eddy correlation method, at the Harvard Forest in central Massachusetts have shown that anomalous weather over 1 or 2 months of the year can have a significant impact on annual ecosystem productivity [Goulden et al., 1996; Wofsy et al., 1993]. They observed variability in NEP due to changes in growing season length (controlled primarily by spring and fall temperatures), snow depth and snow pack duration (affecting winter soil temperatures and soil respiration), drought in summer, and summer cloud cover; NEP at their temperate forest site ranged from 1.4 to 2.8 t C ha^{-1} yr^{-1} [Goulden et al., 1996].

In this paper, a process-oriented model of boreal, black spruce/moss forest ecosystem productivity [Frolking et al., 1996] is used to examine the sensitivity of annual NEP to seasonal anomalies in weather. By resolving annual weather anomalies into their daily manifestations and by accounting separately for the potentially different responses of the various components of the ecosystem carbon balance (tree, moss, decomposition), this study explores how annual ecosystem NEP, as the sum of its components, is influenced by seasonal anomalies in weather. This model was developed in conjunction with the Boreal Ecosystem-Atmosphere Study (BOREAS), a large-scale, interdisciplinary effort to investigate how the interaction of climate/weather and the boreal ecosystem influences the exchange of energy, water, and carbon between the terrestrial biome and the atmosphere [Sellers et al., 1995].

Model Description

The spruce-and-moss (SPAM) model links four, daily time step submodels (soil climate, tree NPP, moss NPP, and decomposition) to simulate daily NEP for spruce/moss boreal forest ecosystems. The model has been described in detail elsewhere [Frolking et al., 1996], and only a brief summary is provided here. The soil profile in the model consists of a green moss layer (3 cm) over a litter layer (~3 cm), over a humus layer (~20 cm), over clay mineral soil (150 cm). The soil climate submodel keeps track of a snowpack depth and water content, soil water and ice contents, and soil temperature profiles. Air temperature controls the partitioning of precipitation into snow and rain and also, along with day length, controls daily rates of snow melt. Soil temperature is simulated as a daily time step heat diffusion problem, using the apparent heat capacity method to track soil water phase changes. Soil moisture dynamics are simulated with a modified bucket model for the thick surface organic horizon (moss plus peat) and a simplified Richard's equation for the underlying mineral soil.

The tree and moss NPP submodels calculate daily photosynthesis as an optimal rate modified by empirical functions of daily average photosynthetically active radiation (PAR), daytime air and moss temperature, soil or moss water status, and vapor pressure deficit (affecting trees only). Foliar respiration is calculated as a base rate, modified by daytime and nighttime average temperatures and, for the moss, water content. Pho-

tosynthesis and foliar respiration calculations are made for 20 tree and 20 moss canopy layers. PAR is attenuated exponentially by leaf area in the tree canopy and by leaf mass in the moss canopy, and a temperature gradient is calculated for the moss. The photosynthetic response to PAR intensity is modeled as a rectangular hyperbola, with half saturation values of 200 μE m^{-2} s^{-1} for spruce [Aber and Federer, 1992] and 40 μE m^{-2} s^{-1} for moss [Busby and Whitfield, 1978]. The temperature response function is parabolic, with an optimum at 15°C for spruce [Sveinbjornsson, 1992], and increasing from 15°C to 20°C over the growing season for the moss [Skre and Oechel, 1981]. (This is the only ecophysiological acclimation included in the model.) Moss photosynthesis response to water content is also parabolic, with an optimum at 4.5 grams water per gram dry matter [Busby and Whitfield, 1978; Skre and Oechel, 1981]. The soil water content multiplier for spruce photosynthesis drops linearly from 1 to 0 as liquid water in the rooting zone drops from 70% of field capacity to the wilting point. Sapwood respiration is calculated as a base rate per unit volume, multiplied by a temperature factor and stand sapwood volume [Ryan et al., 1995]; tree root respiration is a function of root nitrogen content and root temperature [Ryan, 1991], where root biomass was an input parameter and a root C:N ratio of 45 was used [Hendricks, 1994]. Initial biomass and rates of optimal photosynthesis and base respiration are specified as input parameters (Table 1); site-specific properties were taken from BOREAS field data where possible, while process rates were derived from earlier studies reported in the literature. In this way the model was not specifically tuned to a particular site.

The decomposition submodel treats a series of vertically stratified, annual litter cohorts (needle plus moss, up to 34 years old in this case). The base rate of decomposition (Table 1) of each litter cohort declines linearly as the cohort loses mass. Like a standard first-order decay model, under the assumption of uniform conditions in the recent past, this formulation has an analytical solution for the remaining litter cohort mass as a function of age, which is used for model initialization [Frolking et al., 1996]. During simulation, actual decomposition rates are the product of the base daily rate times reduction factors calculated from the daily litter-layer temperature (exponential function Q_{10} = 2) and moisture content (linear decline below and above an optimum range). A single humus pool contains all litter older than 34 years; it decomposes at a constant base rate (0.0125 yr^{-1}), modified by the daily humus-layer temperature and moisture content. Fine-root turnover is set at 0.25 yr^{-1}, and the initial root litter pool is in equilibrium with this. A series of vertically (but not age) stratified, fine-root litter pools decompose at a constant base rate (0.125 yr^{-1}), modified by the daily soil temperature and moisture contents down the soil profile.

The SPAM model is driven by daily weather, using maximum and minimum air temperatures, total precipitation, relative humidity, and daytime average incident photosynthetically active radiation (PAR). SPAM outputs are daily values of soil temperature and moisture profiles, gross photosynthesis of both the spruce and the moss, and ecosystem respirations (moss; spruce foliage, sapwood, and roots; the soil litter, humus, and mineral layers). The components of the daily carbon balance are combined to give daily values of spruce and moss NPP, soil respiration, NEP, total gross photosynthesis, and total ecosystem respiration. Daily values are summed to give annual carbon balance values for each of these components.

Table 1. SPAM Model Initial Carbon Pools and Rates

component	value	units	reference[a]
Spruce			
root biomass	400	$g\ C\ m^{-2}$	site data[a]
sapwood volume	0.0083	$m^{-3}\ m^{-2}$	site data[a]
maximum foliar biomass	400	$g\ C\ m^{-2}$	site data[a]
Soil			
total organic mass	12000	$g\ C\ m^{-2}$	site data[b]
Moss			
biomass	500	$g\ C\ m^{-2}$	site data[b]
Peat			
litter mass	620	$g\ C\ m^{-2}$	internal calculation[c]
humus mass	9900	$g\ C\ m^{-2}$	site data[b]
Mineral Soil			
organic carbon	80	$g\ C\ m^{-2}$	internal calculation[c]
Rates			
spruce photosynthesis	18.9	$nmol\ g^{-1}\ s^{-1}$	*Hom and Oechel* [1983]
foliar respiration	1.89	$nmol\ g^{-1}\ C\ s^{-1}$	*Aber and Federer* [1992]
sapwood respiration	15	$mmol\ C\ m^{-3}\ s^{-1}$	*Ryan et al.* [1995]
root respiration	0.0106	$mol\ C\ mol^{-1}\ N\ h^{-1}$	*Ryan* [1991]
moss photosynthesis	1.0	$mg\ CO_2\ g^{-1}\ h^{-1}$	*Skre and Oechel* [1981]
moss respiration	0.11	$mg\ CO_2\ g^{-1}\ h^{-1}$	*Skre and Oechel* [1981]
initial decomposition	0.125	yr^{-1}	*Berg et al.* [1993]

[a]Preliminary site data collected by T. Gower, University of Wisconsin (TE-6)
[b]Preliminary site data collected by J. Harden, United States Geological Survey (TGB-12).
[c]See *Frolking et al.* [1996].

Variability in Ecosystem Carbon Balance: 1994 and 1995

One of the BOREAS study sites was an even-aged (80 year old), mature black spruce (*Picea mariana*) stand near Thompson, Manitoba, within the BOREAS northern study area (NSA) (site is called NSA-OBS, 55°52′N, 98°29′W). The site has a nearly continuous ground cover of moss (generally *Pleurozium schreberi*, *Hylocomium splendens*, or *Sphagnum* spp.). A meteorological station installed at Nelson House, about 9 km northwest of NSA-OBS, has generated a nearly continuous record of air temperature, precipitation, relative humidity, PAR, as well as a suite of other meteorological variables for 1994 and 1995, all recorded at 15 min intervals [*Shewchuk*, 1996]. For the analysis presented here, gaps in this record (due to instrument problems) were filled with data from an identically instrumented meteorological station at the Thompson Airport (40 km east of NSA-OBS), and daily averages were constructed.

The SPAM model simulated the daily carbon balance of the NSA-OBS site (as a black spruce/feathermoss ecosystem) for 1994 and 1995. Where possible, initialization parameters for site carbon pools were taken from data collected at the site during the BOREAS campaign (Table 1). Because weather data were not collected at this site during 1993, the simulation began with two years of 1994 weather data to equilibrate the soil climate submodel, followed by 1994 and 1995 daily weather data to generate model output. Thus the simulated snowpack and soil temperatures on January 1, 1994, resulted from November and December 1994 weather conditions.

Air temperature in 1994 was generally above 30 year normals for September through December and was warmer than normal in June 1995; both years were warmer than normal in March (Figure 1a). Both 1994 and 1995 had about 400 mm of precipitation (1951–1980 mean is 550 mm), but the precipitation patterns were quite different for the two years (Figure 1b). In 1994, precipitation was near normal for January through mid-July and then quite low for the remainder of the year.

March through July 1995 was extremely dry, August was very wet, September and October were dry, and November and December were near normal.

Simulation results for 1994 were compared to preliminary field measurements from the 1994 BOREAS field campaign [*Frolking et al.*, 1996]. Simulated soil temperatures were in
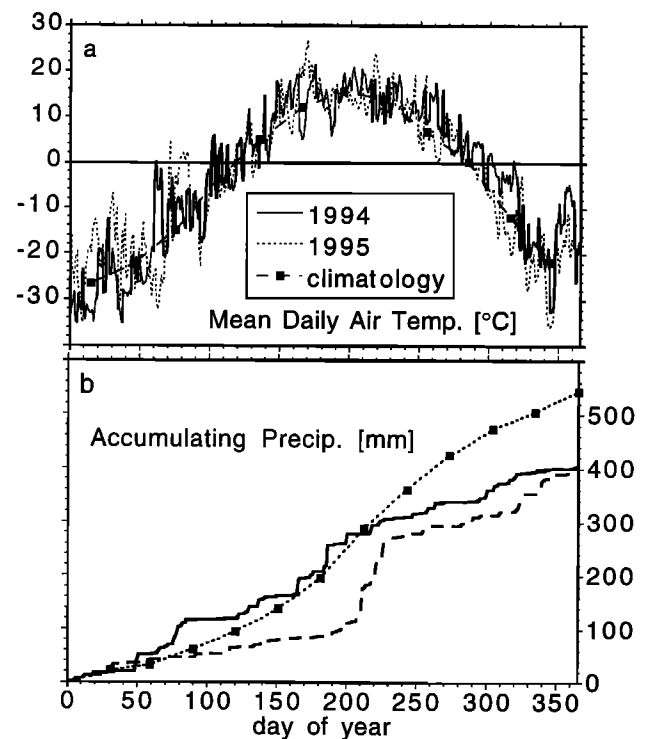

Figure 1. (a) Mean daily air temperature and (b) accumulating daily precipitation for 1994 and 1995 compared with 1951–1980 mean monthly climatology. Both years were drier than normal, but with very different timing of precipitation.
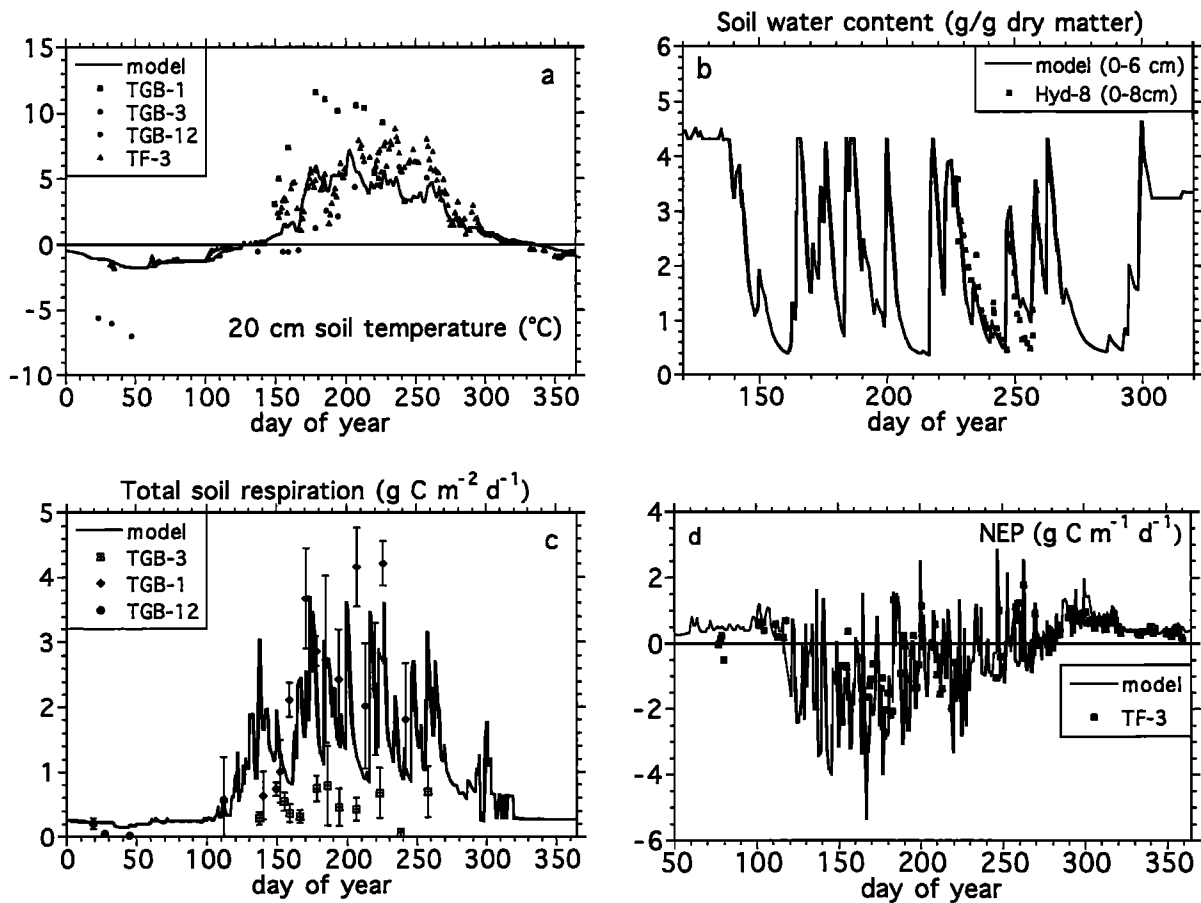
Figure 2. Simulated and measured (a) 20 cm soil temperature; (b) 0–7 cm water content; (c) soil respiration; and (d) daily net ecosystem production (NEP) (NEP $<$ 0 implies carbon uptake by the ecosystem). Preliminary soil water data are from BOREAS team HYD-8. Preliminary soil respiration data are from Boreal Ecosystem-Atmosphere Study (BOREAS) teams TGB-12 [*Winston et al.*, 1995], TGB-3, and TGB-1. Preliminary NEP data are from BOREAS team TF-3. Reprinted with permission from *Global Change Biology*, 2(4), 343–366 (see *Frolking et al.* [1996] for more details).

general agreement with measured temperatures, which displayed a wide range of variability. At 20 cm, model soil temperatures were slower to warm in the spring and cooler during the summer than most observations (Figure 2a). The water content of the surface organic layer was characterized by rapid wetting and gradual drying (Figure 2b). Water contents of the deeper peat and underlying mineral soil were less dynamic. SPAM soil respiration results (moss plus roots plus decomposition) were comparable with but nearer the high end of the observed range of total soil respiration measurements made with opaque, static chambers at the same site (Figure 2c); model NEP was generally consistent with the tower observations, both for seasonal course and for annual total (Figure 2d). *Frolking et al.* [1996] also presented model simulations of interannual variability in NEP for 1967–1989, driving the SPAM model with observed, daily meteorological data collected at the Thompson, Manitoba, airport by the Canadian Atmospheric Environment Service. Their results indicated that while the forest was a carbon sink for all but one of the simulated years, annual NEP could vary by more than 100% from its 20 year mean. The timing of snowmelt and ground thaw in the spring had a major impact on simulated annual NEP for this northern latitude, evergreen forest.

Simulated spruce NPP was similar during the winter periods

of both 1994 and 1995 (day-of-year less than 100 or greater than 300), with respiration rates (foliage + wood + roots) of 0.2–0.5 g C m^{-2} d^{-1} (Figure 3a). Spring onset of net carbon uptake (NEP $<$ 0) occurred at the end of April in both years. NPP for spruce was similar for the early and late summers of both years. From mid-June through July, however, spruce NPP was generally smaller in 1995, with the major difference during a very hot, dry period around day 170 when spruce respiration equaled or exceeded photosynthesis for about 1 week. Soil water limitations reduced photosynthesis for about 30 days in 1995 (days 180–210). Simulated annual spruce NPP was 139 g C m^{-2} in 1994 and 112 g C m^{-2} in 1995.

The pattern of simulated NPP for the feathermoss was quite different for 1994 and 1995 (Figure 3b). In 1994 there was a 2 week period of metabolic respiration while the moss was still snow covered; in the SPAM model, moss respiration and photosynthesis both occur at temperatures greater than $-1°C$; light attenuation in the snowpack limited photosynthesis during this period. After the onset of productivity following snowmelt, the moss alternated between periods of productivity (NPP $<$ 0), "dormancy" (NPP $\sim$ 0), and carbon loss (NPP $>$ 0). "Dormancy" occurred during extended dry periods. Nonvascular plants like feathermoss rely on moss "canopy" storage of precipitation and snowmelt as their only water source and

during summer dry by evaporation within a few days following a wetting [Busby et al., 1978]. Unlike most vascular plants, mosses are able to reduce respiration losses (along with photosynthetic gains) at times of water limitation [Longton, 1988], so NPP declines to near zero. Days with significant carbon loss (NPP > 0) occurred in both years and were generally associated with rainy days (low PAR) or very warm days, while the moss was still wet and metabolically active. Simulated annual moss NPP was 13.0 g C m^{-2} in 1994 and 9.7 g C m^{-2} in 1995.

Simulated heterotrophic respiration associated with decomposition had a background level of about 0.2 g C m^{-2} d^{-1} during the winter months of 1994 and 1995 (Figure 3c). Rates roughly tripled during the summer months, with dry periods causing reduced decomposition rates. This effect was especially strong in the early summer of 1995. Simulated annual respiration from decomposition was 126 g C m^{-2} in 1994 and 130 g C m^{-2} in 1995.

Overall, the ecosystem reversed from being a carbon source (NEP > 0) to a carbon sink (NEP < 0) at the end of April in both 1994 and 1995, though the forest had a more sustained carbon uptake early in the 1995 growing season (Figure 3d). Simulated NEP in 1995 was near zero from mid-June through July due to the drought. In both years, NEP tapered off in late summer as air and soil temperatures cooled and day length shortened, and the ecosystem reverted to a carbon source by the end of September. Simulated annual NEP was −26.3 g C m^{-2} in 1994 and −2.5 g C m^{-2} in 1995 (negative NEP implies carbon uptake by the ecosystem).

Simulated gross carbon fluxes (moss plus spruce gross photosynthesis; moss plus spruce plus heterotrophic respirations) highlight several features of the ecosystem carbon balance. Unstressed photosynthesis in this evergreen forest (spruce and moss) rose to peak values of 7–8 g C m^{-2} d^{-1} during May (days 120–150) and maintained those values through August (Figure 4). Respiration rates were slower to rise in the early summer and were roughly equal to photosynthesis by the end of the summer. Thus ecosystem productivity was skewed toward the early part of the growing season. The model probably overestimates early summer productivity because it does not simulate an early growing season phenological limit on maximum photosynthetic rate, which was indicated by the tower NEP measurements (M. Goulden, personal communication, 1996; also see Figure 2d). There was a high degree of variability (generally synchronous) throughout the growing season for both photosynthesis and respiration (Figure 4). Significant drops in metabolic activity tended to co-occur in photosynthesis and respiration and were generally associated with dry conditions. Dry conditions quickly reduced moss metabolic rates, more slowly reduced heterotrophic decomposition, and an extended drought reduced spruce photosynthesis. The SPAM model results imply that though the overall NPP of the moss was fairly small in both years, it played a significant role in gross carbon fluxes. Annual gross photosynthesis was 657 g C m^{-2} in 1994 and 632 g C m^{-2} in 1995; annual total respiration was 630 g C m^{-2} in 1994 and 629 g C m^{-2} in 1995. Overall carbon balances for both years (and 1975, the base year for sensitivity studies presented below) are summarized in Table 2.

Because of extended dry periods during the late summer of 1994 and the early summer of 1995, simulations for both of those years had lower productivity than the means of a 1968–1989 simulation [Frolking et al., 1996]. Assuming an annual litterfall for the spruce of 140 g C m^{-2} (needles plus roots), the spruce did not have any net growth in 1994 or 1995 but aver-
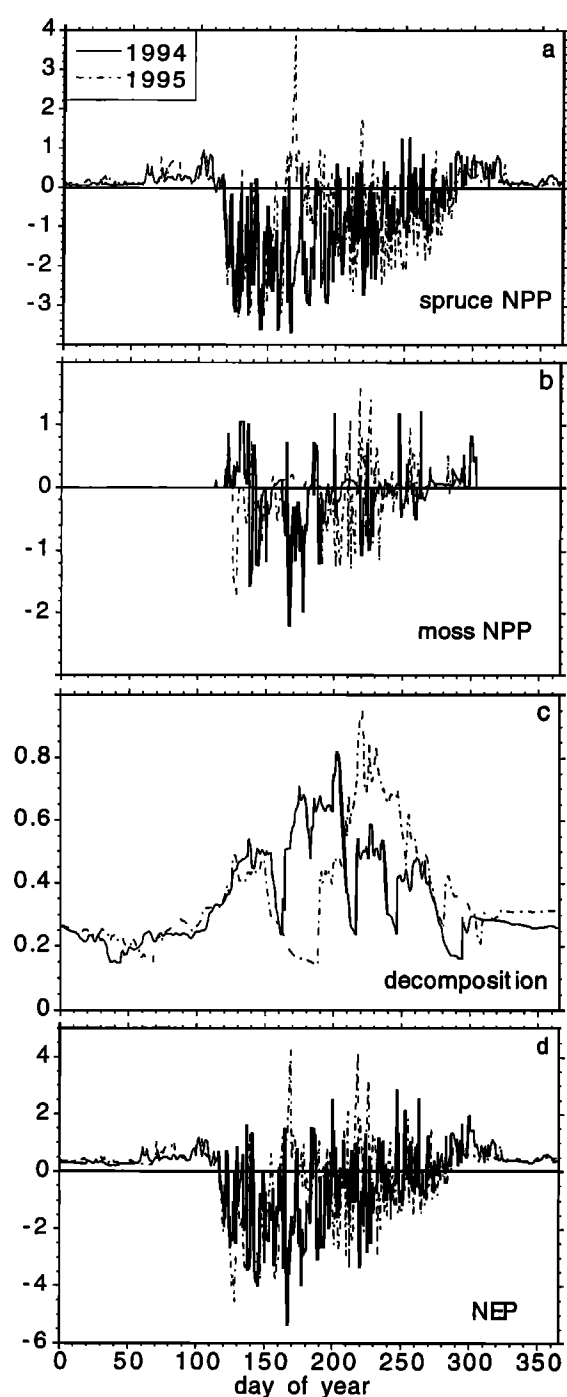

Figure 3. Comparison of 1994 (solid line) and 1995 (dashed line) simulated daily (a) spruce net primary productivity (NPP), (b) moss NPP, (c) decomposition (heterotrophic respiration), and (d) NEP for a black spruce/moss forest near Thompson, Manitoba (NSA-OBS). Note that vertical scales are different for each panel. Early summer in 1995 was very dry (see Figure 1b); this caused reductions in all components of the carbon balance for days 165–210. Total annual simulated carbon fluxes are listed in Table 2.

aged 70 g C m^{-2} for 1968–1989, comparable to mean annual tree productivity for black spruce forests in central Alaska [Viereck et al., 1983]. Feathermoss NPP was also lower for 1994 and 1995, but the 1968–1989 mean of 35 g C m^{-2} was comparable to reported values for Canada (16–60 g C m^{-2} [Weet-
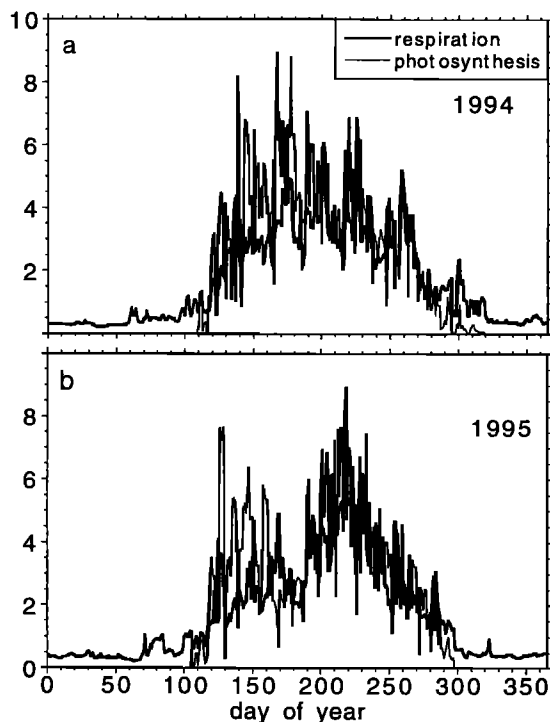
Figure 4. Simulated daily total gross photosynthesis (light line) and total respiration (heavy line) for a spruce/moss forest in (a) 1994 and (b) 1995. Once photosynthesis began in the spring, it generally exceeded respiration until late summer; the photosynthesis curve was skewed toward early summer (following day length and insolation), while the respiration curve peaked later in the summer (following air and soil temperatures). Respiration occurred throughout the year. Both photosynthesis and respiration were reduced during the drought in the early summer of 1995.

Figure 5. Daily accumulating (a) degree days and (b) precipitation for 1975 (bold line) and 1970–1974, 1976–1989 (thin lines) for Thompson, Manitoba. 1975 was generally a "normal" weather year, with a slightly wetter than average summer.

man and Timmer, 1967]) and Scandinavia (12–65 g C m^{-2} [*Tamm*, 1953]), and at the low end of values reported for central Alaska (36–60 g C m^{-2} [*Oechel and Van Cleve*, 1986]). The SPAM model results were generally consistent with unpublished 1994 and 1995 tower flux data from the NSA-OBS site for daily gross carbon fluxes, the seasonal cycle of photosynthesis and respiration, and for annual totals [*Frolking et al.*, 1996; M. Goulden, personal communication, 1996]. The principal differences were that SPAM gross photosynthesis early in the growing season was higher than tower observations, the drops in gross photosynthesis were overpredicted by SPAM for the dry periods, and annual NEP predicted by the model was somewhat greater than tower estimates.

Seasonal Sensitivity of the Ecosystem Carbon Balance

A series of simulations was conducted with 2 month temperature and precipitation anomalies. The base weather year for these simulations was 1975 (weather data from the Thompson, Manitoba, airport collected by the Canadian Atmosphere Environment Service; daily weather file provided by Joseph Coughlan, NASA Ames). Both air temperature and precipitation in 1975 were near long-term means, with no clear periods of abnormal weather (Figure 5); the 1975 growing season was relatively wet and had no extended dry periods. SPAM simulated carbon exchanges for ecosystem productivity and its com-
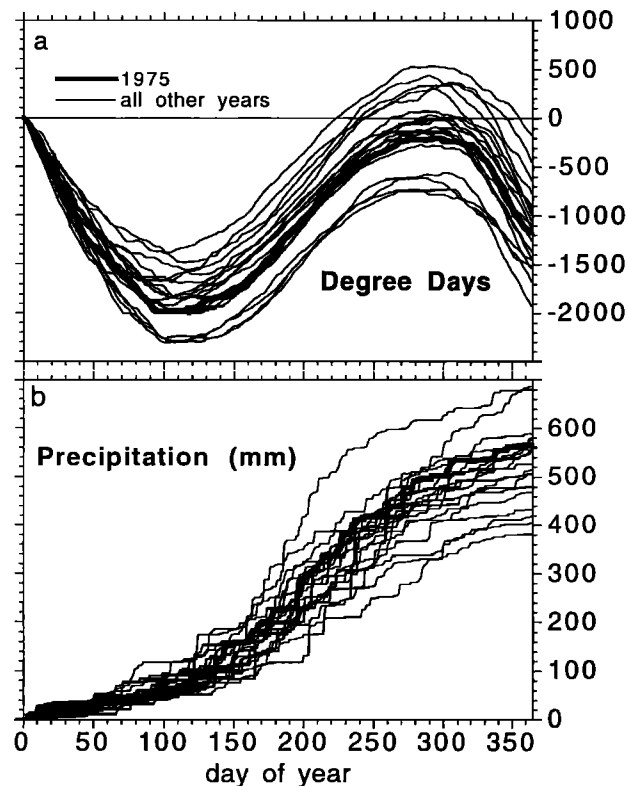
ponents were higher in 1975 than either 1994 or 1995 (Table 2), due to abundant precipitation throughout the summer and an earlier snowmelt in 1975.

Four sets of six anomalous weather scenarios were generated. In the first set of six simulations, maximum and minimum daily air temperatures were raised by 3.5°C for two consecutive months (midwinter, January and February; late winter, March and April; early summer, May and June; summer, July and August; fall, September and October; and early winter, November and December). In the second set of six simulations, daily air temperatures were lowered by 3.5°C for each 2 month interval; in the third set the amount of precipitation on each day of each 2 month interval was doubled, and in the fourth set the amount of precipitation each day was reduced by half. These scenarios are generally consistent with observed weather variability for Thompson, Manitoba (Table 3). None of these scenarios involved changing the number nor sequence of days

Table 2. Annual Carbon Fluxes From the SPAM Model

Component	Carbon Flux, g C m^{-2}		
	1994	1995	1975
Spruce NPP	139	112	205
Moss NPP	13	10	40
Decomposition	126	130	180
NEP	27	3	66
Total photosynthesis	657	632	816
Total respiration	630	629	750

NPP, net primary productivity; NEP, net ecosystem production.

Table 3. Mean and Range (1968–1989) of 2 Month Average Temperatures (°C) and Total Precipitation (mm) for Thompson, Manitoba

Months	Mean Temp	Temp Range (max/min)	Total Ppt	Precip Range (max/min)
Jan. and Feb.	−23.1	−17.4/−28.9	35	56/12
March and April	−7.8	−4.2/10.8	48	83/23
May and June	9.2	12.5/5.3	118	227/40
July and Aug.	14.9	17.4/11.5	159	285/76
Sept. and Oct.	4.4	6.6/1.6	116	251/67
Nov. and Dec.	15.6	−10.4/−22.1	60	121/22

Data provided by the BOREAS project. Temp, temperature; Ppt, precipitation.

with precipitation from the 1975 base year. The simulated daily PAR values also were unchanged from the 1975 base year (no PAR data were available, so daily PAR was calculated as a function of diurnal air temperature range, developed from 1994 field data [*Frolking et al.* [1996]; this range was unaffected by the anomalies used). Comparisons were made for the magnitudes of annual NPP of spruce and moss, annual decomposition, and annual NEP.

Patterns for spruce and moss NPP deviations from the 1975

base year simulations for temperature anomalies were similar (Figures 6a and 6b). The largest changes for both were a decrease in NPP for warmer summers (July and August) and an increase in NPP for cooler summers. These resulted from model temperature dependencies of photosynthesis and plant respiration. The combination of these two effects led to a fairly strong temperature dependence in the vicinity of 20°C; mean daytime air temperature for June through August 1994 and 1995 was 18°C at the NSA-OBS site. Increasing air temperatures greatly reduced photosynthesis and increased respiration, causing significant decline in NPP for both the spruce and the moss, while lowering temperatures had the opposite effect. This strong temperature dependence was not observed in the eddy correlation tower flux data from the NSA-OBS site, which showed a much broader ecosystem NPP maximum at 15°–25°C [M. Goulden, personal communication, 1995], so the model has probably overemphasized ecosystem sensitivity to warm temperatures. This discrepancy may arise from using functional relationships based on leaf and/or branch studies to describe stand-scale ecophysiological behavior, which is generally more linear [e.g., *Ruimy et al.*, 1995].

Both moss and spruce showed increased NPP for a warmer spring (March and April) and decreased NPP for a cooler spring (Figures 6a and 6b). This was the result of an earlier snowmelt, ground thaw, and onset of the growing season for
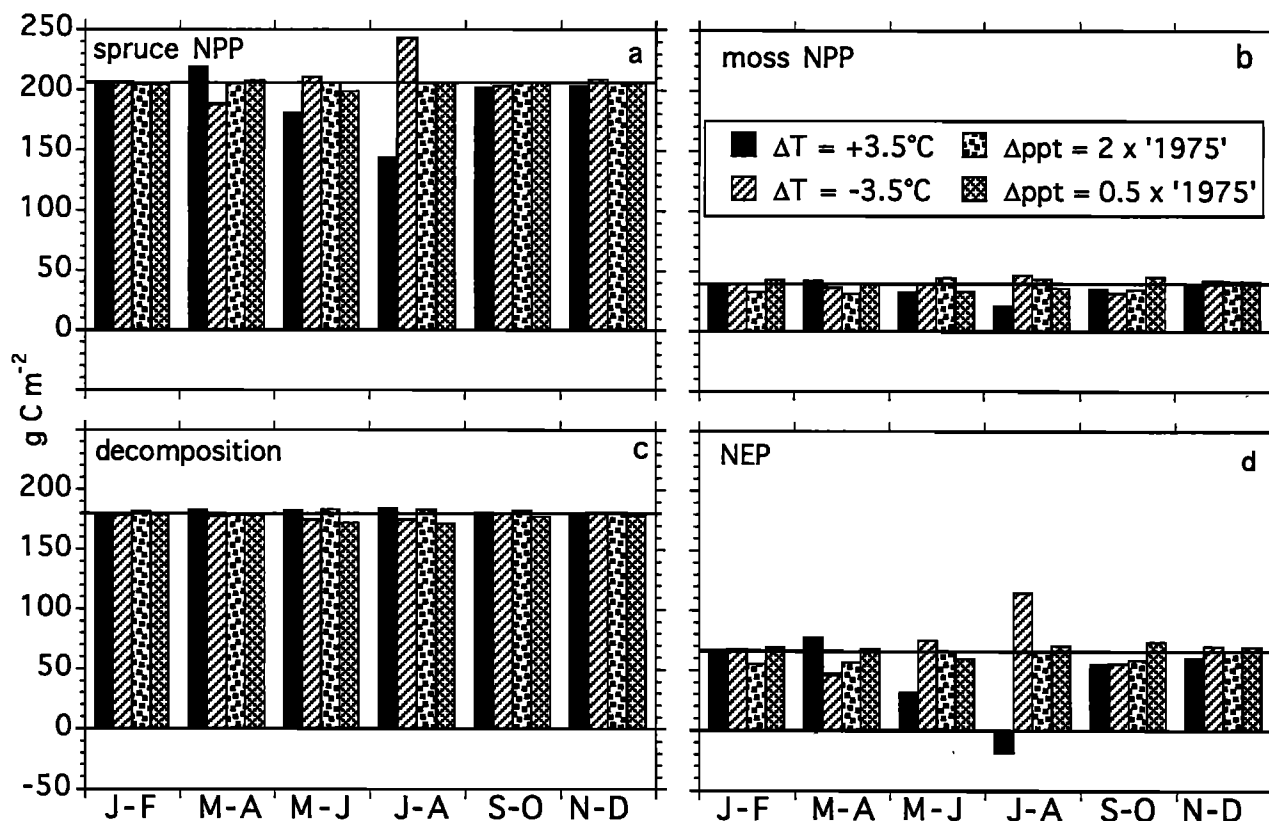

Figure 6. Magnitude of annual simulated carbon fluxes (in grams C per square meter) for 24 anomalous years. Note that the normal sign convention is not used, and all carbon fluxes are portrayed as positive, so in this figure carbon uptake is given as positive NEP. Bars represent result of 2 month air temperature anomalies: +3.5°C (stippled bars) or −3.5°C (diagonally striped bars); or 2 month precipitation anomalies: doubled (mottled bars) or halved (hatched bars) on (a) spruce NPP, (b) moss NPP, (c) heterotrophic respiration (decomposition), and (d) NEP. In each case the weather anomalies lasted for two consecutive months (January–February; March–April; May–June; July–August; September–October; or November–December). Horizontal lines in each plot represent 1975 base run values.

the warmer spring, and later for the cooler spring. Fall and winter temperature anomalies had little impact on the spruce NPP. For the moss however, warmer temperatures in fall (September and October) reduced NPP by delaying the freeze-up of the moss and thus allowing it to respire further into the fall, when light levels (and photosynthesis) were low. Cooler temperatures in the fall also reduced moss NPP by generating an early and deep snowpack, which insulated the moss from freezing and enhanced respiration. Cooler early winter temperatures increased moss NPP by eliminating a week of respiration in early November (which had no snow cover and air temperatures greater than 0°C in 1975).

Warm temperature anomalies increased heterotrophic respiration (decomposition) by 1–5% in all nonwinter cases (Figure 6c). Cooler temperatures reduced decomposition in the spring and summer, but decomposition increased slightly with cooler early winter temperatures because the earlier and/or enhanced snow pack better insulated (and effectively warmed) the soil. In this spruce/moss forest temperature effects on decomposition appear to be damped due to the insulating effects of the snow pack for about half the year and also by the insulating effects of the near-continuous ground cover of moss overlying the organic and mineral soil.

Because temperature effects on decomposition were relatively small and because both spruce and moss behaviors were generally similar, temperature anomaly effects on overall NEP followed the spruce and moss changes, with dramatic effects for midsummer temperatures (Figure 6d). Again, this sensitivity to summer temperatures may be exaggerated in the model, due to stand-scale smoothing of leaf and branch scale behaviors. Nonetheless, it is clear that the impact of a warmer or cooler climate would depend on the time of year during which the majority or the warming or the cooling occurred. There appears to be no simple relationship between mean annual air temperature (the same for all of the positive or the negative anomalous temperature runs) or mean annual growing season temperature and annual NEP. The effect of temperature anomalies in this ecosystem appears to be much stronger on vegetation productivity than on decomposition rates.

Anomalous precipitation effects on ecosystem carbon fluxes in these scenarios were generally small. Because precipitation was abundant in 1975 and there were no long dry spells, the spruce never suffered from soil water limitations, even in the anomalously dry summer simulations. Increased winter (January and February) precipitation did reduce spruce NPP slightly (Figure 6a) by generating a deeper snowpack and thus a later spring thaw. The largest effects on moss NPP were reductions caused by enhanced winter snow fall (January–April) which caused a later snowmelt and thus enhanced spring respiration before the onset of photosynthesis (Figure 6b). Enhanced fall precipitation also reduced moss NPP by insulating the respiring moss from cold temperatures, while reduced fall precipitation enhanced moss NPP by allowing the moss to freeze more quickly. Reduced summer precipitation caused some reduction in moss NPP due to occasional drying and dormancy in July and August, while reduced winter precipitation enhanced NPP by leading to an earlier snowmelt and onset of the growing season.

Decreases in summer precipitation reduced decomposition rates, while increases in precipitation led to a slight increase (Figure 6c). The overall impact of increased precipitation during the winter was to reduce NPP by enhancing the snow cover (Figure 6d). Increased precipitation in the summer caused increases in both moss NPP and decomposition, with little change in NEP (Figure 6d). Reduced winter precipitation enhanced NEP by reducing the snowpack; less rain in May and June reduced NEP, while less rain in July and August enhanced NEP (Figure 6d).

Drought Sensitivity of the Ecosystem Carbon Balance

A series of month long drought simulations, again with 1975 Thompson weather as a base year, explored the sensitivity of the spruce/moss forest carbon balance to extended dry spells, such as occurred in 1995. In these seven simulations, each day with precipitation in one month (April through October) had its precipitation set to zero, and its daily maximum and minimum air temperatures set to the mean values of all nonprecipitation days of that month. The resetting of maximum and minimum daily air temperatures, coupled with the model's regression relationship between PAR and diurnal temperature range, assured that "drought" days were relatively "sunny," though never excessively hot. Simulated drying of the surface organic layers of the soil in the SPAM model follows an exponential decay to minimum water content, with decay times and initial lags increasing down the profile (moss < litter < humus). Water loss is limited to total potential evaporative demand for the day (calculated with the Thornthwaite equation) minus spruce transpiration (calculated as net productivity times water-use-efficiency). In midsummer simulations the feathermoss dried within about five days, the litter layer within about 8 to 10 days, and the much thicker humus layer of these simulations took longer than a month to completely dry out. Drying rates were slower early and late in the growing season.

April droughts had little effect on any component of the ecosystem carbon balance (Figure 7) because the soil was snow covered for most of April, so little drying occurred, and April 1975 was a fairly dry month, so imposing a drought did not reduce the snowpack very much. Summer month droughts and subsequent soil drying reduced spruce NPP by 10–15%. Because the moss dries so rapidly, after several days into a drought month the moss became "dormant" and weakly respiring. Moss NPP was thus reduced for droughts in those months in which the moss was gaining carbon in the base run (May through August), and moss NPP was increased for droughts in September and October when the moss was losing carbon in the base run (Figure 7b). Annual decomposition was reduced by about 5–10% due to drying of the litter layer for droughts in all months except April (Figure 7c). The net effect of a month long drought on the ecosystem carbon balance was a reduction in NEP (and its components) for summer droughts, and an increase in NEP for fall droughts, due to enhanced moss NPP and small changes in the other components (Figure 7d).

In two final simulations the growing season precipitation for 1975 (a total of 381 mm in 73 rainstorms from day 125 to day 275) was redistributed into a series of frequent small rainstorms (7.6 mm of precipitation every 3 days) and a series of infrequent rainstorms (25.4 mm every 10 days). There was no change in spruce NPP between either of the simulations and the base run (Figure 8a). Moss NPP dropped by 50% for the growing season with infrequent, large rainstorms and increased by about 50% in the frequent, small rainstorm case (Figure 8b). In the base run simulation the moss experienced eight dry spells during the growing season, often several days long. With
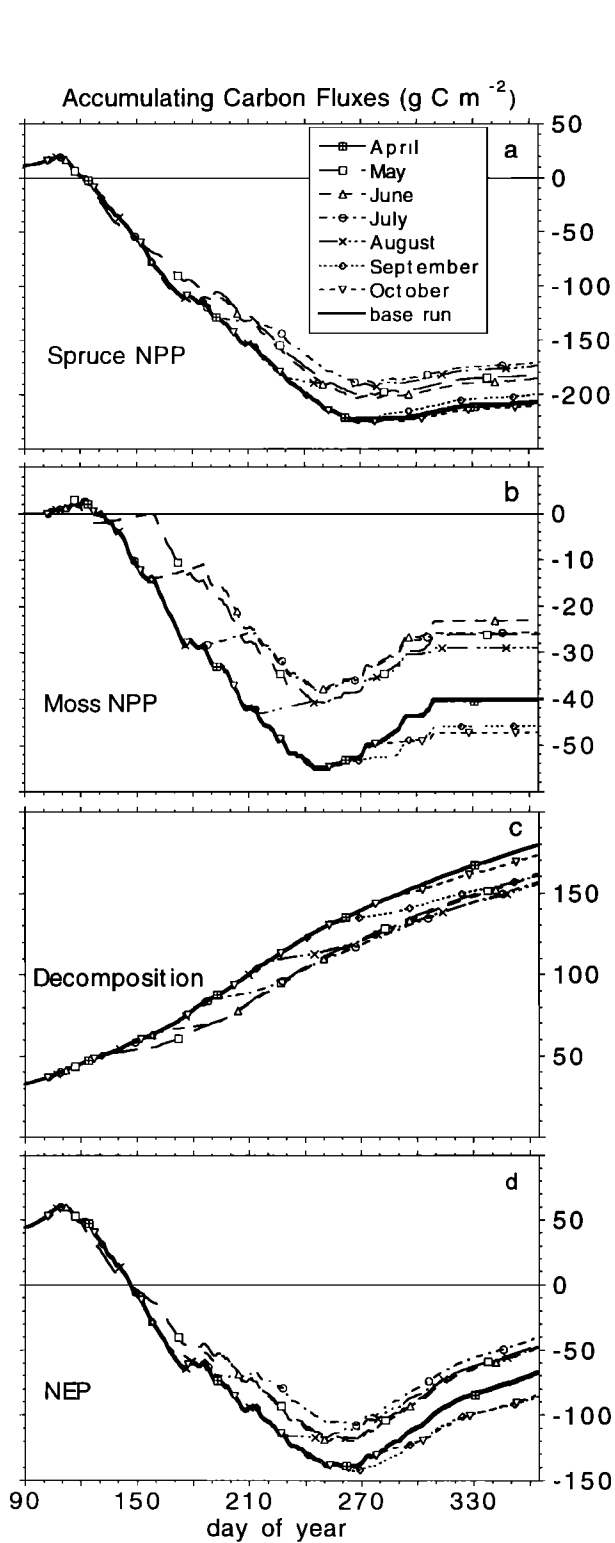
Figure 7. Simulated annual accumulating carbon fluxes for 1975 (base year; heavy solid line) and seven anomalous years for (a) spruce NPP, (b) moss NPP, (c) decomposition, and (d) NEP. Note that the vertical scales are different for each panel and that the horizontal axis begins with day 90 (April 1). In each anomalous year the base year weather file was modified to have a single month of drought (April–October), in which all precipitation was set to zero.
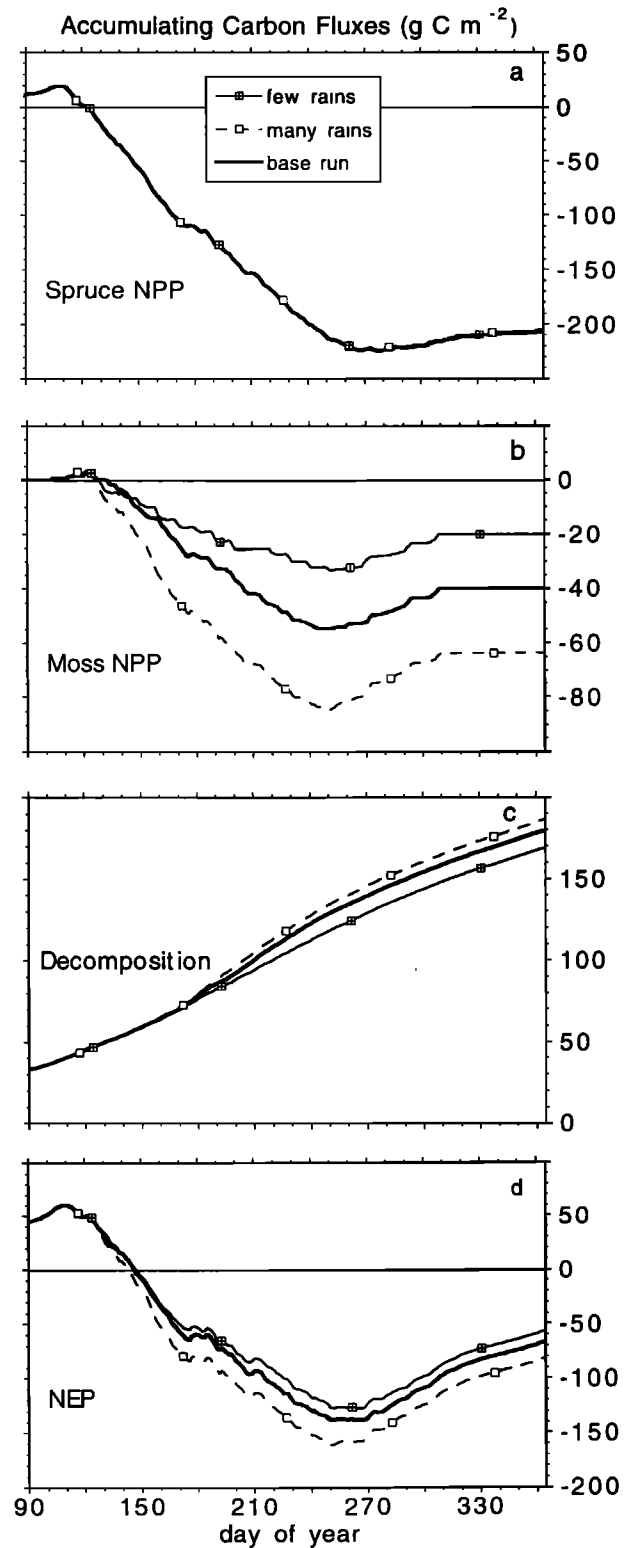
Figure 8. Simulated annual accumulating carbon fluxes for 1975 (base year; heavy solid line) and two anomalous years for (a) spruce NPP, (b) moss NPP, (c) decomposition, and (d) NEP. In one case the 1975 growing season precipitation was redistributed into a series of frequent, small rainstorms (short dashed line); in the other case it was redistributed into a series of infrequent, large rainstorms (light solid line). There was no change in total precipitation over the growing season or the year. Note that the vertical scales are different for each panel and that the horizontal axis begins with day 90 (April 1).

the frequent rainstorm scenario the moss never dried completely during the summer; this enhanced both early summer net growth and late summer net respiration. With the infrequent rainstorm scenario the moss was dry for about 5 days of every 10 days. Annual respiration associated with decomposition increased slightly with more frequent rainstorms and decreased by about 5% with less frequent rainstorms (Figure 8c). The litter layer dried once during the 1975 base run for about 10 days. It did not dry with the frequent rainstorm scenario and dried between each rainstorm during the summer with the infrequent rainstorm scenario but generally only for 1 to 3 days. The effects of rainstorm frequency on moss productivity and decomposition were opposite with respect to ecosystem NEP, but the effect on the moss was larger so annual NEP decreased by about 15% for the infrequent rainstorm scenario and increased by about 20% for the frequent rainstorm scenario (Figure 8d).

Discussion and Conclusions

The SPAM model simulations presented above suggest that mature black spruce/moss boreal forest stands in northern Manitoba are weak carbon sinks on an annual basis (carbon uptake roughly 0–125 g C m^{-2} yr^{-1} or 0.0–1.25 t C ha^{-1} yr^{-1}).

The nearly complete ground cover of moss, a common feature in the boreal forest [Larsen, 1980], and the long winter snowcover (usually about 6–7 months [Hare and Morley, 1974]) both served to insulate the soil organic matter from variabilities and anomalies in air temperature, so that heterotrophic respiration (decomposition) varied by only up to 5–10% from one scenario to the next. This implies that projections for significantly enhanced soil respiration due to climatic warming [e.g., Robinet, 1994; Jenkinson et al., 1991; Kohlmaier et al., 1990] may overestimate the impact of warming for these ecosystems, as long as the moss remains intact. For disturbed sites with exposed mineral soil and litter (e.g., recent fire scars), a stronger dependence of decomposition on temperature would be expected.

Patterns of spruce and moss NPP sensitivity to anomalous weather were generally similar, though the moss was more sensitive to changes in winter snowcover. Frequency of rainfall during the growing season also influenced moss productivity. Busby et al. [1978] found that feather moss productivity was very dependent on the amount of the growing season during which the moss was wet. While this implies that moss NPP should generally correlate with total precipitation (as Vitt [1990] found for the feathermoss Hylocomium splendens across boreal Canada), rainstorm frequency throughout the growing season can be expected to exert a strong influence [Tamm, 1953]. Greater access to soil water, coupled with generally low water demand, meant that the spruce were less sensitive to month long summer droughts. Model results show both spruce and moss productivity to be quite sensitive to midsummer temperatures.

These sensitivities in the carbon balance of a spruce/moss boreal forest ecosystem highlight three issues in particular. First, multiyear observations are essential to characterize the ecosystem and to test the ability of ecosystem scale models to simulate this variability. Hänninen [1995] distinguished between model precision (level of agreement between prediction and observation of ecosystem function) and model realism (degree of representation of significant causal relationships that control ecosystem function). While perfect realism would

guarantee perfect precision in all cases (and the only perfectly realistic model of an ecosystem is the ecosystem itself), high precision under current conditions guarantees neither a high degree of realism nor a high degree of precision under different conditions. Tests of ecosystem model realism must include both simulations from a variety of sites exhibiting the range of properties that represent an ecosystem and simulations over a number of years that represent the range of weather conditions experienced by an ecosystem. The 5 year measurements of NEP at the Harvard Forest are an excellent example of the value of multiyear observations for quantifying site NEP variability [Goulden et al., 1996]. Oechel et al. [1995] reported that the carbon balance of the wet sedge tundra ecosystem near Barrow, Alaska, switched from a carbon sink in 1972 to a carbon source in 1992. While they made a strong case that this change in direction of the carbon flux can be expected to persist with projected climate change (the summer of 1992 was warmer than the summer of 1972), more observations are needed to confirm this effect and document its persistence. Efforts to establish long-term monitoring in a variety of ecosystems are crucial to our understanding the terrestrial ecosystem carbon balance and will provide essential data sets to test ecosystem model realism.

Second, these results suggest that using variability in annual climatologies (e.g., total annual precipitation, mean annual temperature or biotemperature) to estimate variability in annual ecosystem productivity through simple empirical relationships [e.g., Kojima et al., 1994; Dai and Fung, 1993; Smith et al., 1992] is not likely to be successful. The SPAM model results for ecosystem NEP sensitivity to changes in temperature show more complex behavior than can be captured in simple regression relationships. Warmer fall temperatures tended to reduce moss NPP by delaying freeze-up and prolonging the period of net moss respiration in the fall. Cooler fall temperatures also reduced moss NPP, because they led to the early establishment of an insulating snow cover. The interaction of temperature and precipitation, and their influence on the duration of the snowpack and soil freeze/thaw, plays an important role on annual NEP for the spruce/moss boreal forest. Bonan [1993] argued that it is essential to incorporate details of the interactions between biophysical drivers and ecophysiological responses in order to achieve improved model simulations; he cited several cases where the incorporation of more detail into models led to different simulated ecosystem responses to imposed climate change. Oechel et al. [1995] found that the switch from carbon source to carbon sink in the Alaskan tundra was due to enhanced respiration, but they argued that this was mostly an indirect consequence of higher temperatures; warmer temperatures over several years led to enhanced melting of permafrost (deeper active layer) which facilitated soil drainage. The rise in ecosystem respiration was more directly a result of drier soils and an increased aerobic zone. A simple relationship between soil temperature and soil respiration could not represent this behavior.

Finally, the SPAM model simulations presented here show that consideration must also be given to the pattern of weather throughout the year. The different weather patterns of 1994 and 1995, while generating similar annual climatologies, resulted in different ecosystem behavior for the black spruce/moss forest. Simulations of annual NEP sensitivities to 1–2 month anomalies in temperature or precipitation indicate that the impact of warming in winter, spring, summer, or fall will likely be different; similarly for cooling, wetting, or drying. This

has implications for projections of the impact of climate change scenarios, which generally assume a fairly uniform warming/cooling and wetting/drying throughout the year [e.g., McGuire et al., 1993; Aber and Federer, 1992; Running and Nemani, 1991; Bonan et al., 1990]. More realistic climate change scenarios, which consider changes in means as well as changes in variability and seasonality, can be expected to generate more realistic projections of ecosystem responses [e.g., Mearns, 1995].

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