

Carbon cycling in boreal wetlands: A comparison of three approaches

Susan E. Trumbore,¹ Jill L. Bubier,^{2,3} Jennifer W. Harden,⁴ and Patrick M. Crill²

Abstract. Three independent methods were used to measure net ecosystem production (NEP) in four wetlands near Thompson, Manitoba, Canada. The first method calculated NEP by subtracting heterotrophic respiration from net primary productivity, using both measurements and estimates derived from the literature. The second method used radiocarbon data from cores to derive long-term NEP averaged over the past several decades. The third method used direct measurement of NEP combined with a model to fill in for days with no data. The three methods, with their independently derived uncertainties, all show the same magnitude and pattern of NEP variation across four different wetland types. However, direct measurement yielded distinctly lower estimates of NEP in the most productive sites. Highest NEP ($31 - 180 \text{ gC m}^{-2} \text{ yr}^{-1}$) was observed in the two wetlands with the highest proportion of sedge vegetation. A bog collapse scar and a nutrient-rich fen had NEP values not significantly different from zero. The maximum NEP at sites with intermediate nutrient status is due to slower overall decomposition and is likely associated with greater allocation of production below ground by sedges. The three methods for estimating NEP differ in the effort required, the sources of error, and in the timescale over which they apply. Used in combination, they allow estimation of parameters such as below-ground production and the contribution of heterotrophic decomposition to total soil respiration. Using the radiocarbon method, we also derived estimates of the rate of N accumulation in the four wetland types.

1. Introduction

Boreal wetlands make up a significant portion of the total carbon storage in soils [Gorham, 1991; Schlesinger, 1996]. In Canada these wetlands represent long-term sinks of carbon as they have accumulated since the retreat of the Laurentide Ice Sheet [Harden *et al.*, 1992]. Wetlands of several types have been shown to be currently accumulating carbon [Gorham, 1991; Turunen and Tolonen, 1996] at rates that average about $30 \text{ gC m}^{-2} \text{ yr}^{-1}$. These are higher than C accumulation rates of $3\text{--}20 \text{ gC m}^{-2} \text{ yr}^{-1}$ observed in upland boreal forest sites between fires [Harden *et al.*, 1997; Rapalee *et al.*, 1998]. Little is known about how the carbon balance of wetlands varies with factors such as vegetation or nutrient status, or the evolution of wetlands in zones of discontinuous permafrost regions [Camill and Clark, 1997].

The annual carbon balance for an ecosystem is expressed as net ecosystem production (NEP), the difference between annual net primary production (NPP) (gross photosynthesis (GPP) minus autotrophic respiration (AR)) and heterotrophic respiration (HR):

$$\text{NEP} = \text{NPP} - \text{HR} = \text{GPP} - \text{AR} - \text{HR}. \quad (1)$$

Heterotrophic respiration is that portion of the soil CO_2 efflux derived from decomposition of non-living organic matter. Total soil respiration (TR) consists of HR plus below ground autotrophic respiration (BAR):

$$\text{TR} = \text{HR} + \text{BAR}. \quad (2)$$

Net primary production (NPP) includes both above-ground (ANPP) and below-ground (BNPP) components:

$$\text{NPP} = \text{ANPP} + \text{BNPP}. \quad (3)$$

Measurable quantities in equations (1) – (3) include ANPP (measured by harvesting new plant increment after a 1-year period), instantaneous NEP (measured using clear chambers), gross photosynthesis (GPP), and gross respiration (TR) rates. Other terms have proved difficult to determine directly, especially below ground production (BNPP) and heterotrophic respiration (HR). Annual production by roots is difficult to determine, particularly in wetlands where living sedge roots may penetrate several meters into peat. Total soil CO_2 emissions from wetlands are readily measured using chamber methods. However, the proportion of soil respiration due to heterotrophic respiration, as opposed to metabolic respiration by living plants, is extremely difficult to determine in natural systems.

We used three independent methods to determine NEP for four wetland sites located near the Fen Tower site in the NASA BOREAS (BOreal Ecosystem-Atmosphere Study) northern study area, near Thompson, Manitoba. The first method combined direct measurements of ANPP and soil

¹Department of Earth System Science, University of California, Irvine.

²Complex Systems Research Center, University of New Hampshire, Durham.

³Now at Environmental Studies Program, Mount Holyoke College, South Hadley, Massachusetts.

⁴U.S. Geological Survey, Menlo Park, California.

respiration with literature-based estimates of BNPP and the fraction of soil respiration attributable to organic matter decomposition. The second uses radiocarbon measurements in peat cores to determine decadal and longer-term averaged rates of vertical C accumulation and decomposition. The third, which uses a model to extrapolate direct measurements of NEP to calculate an annual average, is described in detail elsewhere [Bubier *et al.*, this issue].

2. Study Site

The peatland complex in this study was chosen for its diverse representation of plant communities, thermal and hydrochemical gradients, and its inclusion of peat plateaus and collapse scars. The underlying substrates supporting the wetlands are Glacial Lake Agassiz sediments [Teller and Clayton, 1983] overlying the regional bedrock of Canadian Shield Precambrian gneissic granite. Soils are derived predominantly from Glacial Lake Agassiz sediments and consist mostly of clays and organics. Wetlands are common in the region due to poor drainage across the flat terrain. The wetlands include a wide range of types found in northern peatlands from rich fen to bog (pH 7.0 to 3.9) [Zoltai, 1988]. Plant associations in rich fens are diverse, dominated by brown mosses (e.g., *Drepanocladus*, *Scorpidium* spp.) and deciduous shrubs (e.g., *Salix*, *Betula* spp.). Sedges (particularly *Carex* spp.) are common in poor and intermediate fens where water tables are close to the surface. Permafrost underlies many of the peatlands; frozen palsas and peat plateaus are dry and wooded with upland plant communities such as black spruce (*Picea mariana*), feathermosses (e.g., *Pleurozium schreberi*), and ericaceous shrubs (e.g., *Ledum groenlandicum*). Areas of permafrost degradation are found interspersed in the frozen features. These collapse scars become bogs (species poor, *Sphagnum*-dominated communities) if they collapse completely internal to a peat plateau, isolated from groundwater. Alternatively, they may develop into fens if they collapse on the edge of peat plateau where groundwater intrudes [Vitt *et al.*, 1994; Zoltai, 1993; Halsey *et al.* 1997; Camill and Clark, 1997].

Four sites were chosen within the larger peatland complex: rich fen, intermediate fen, poor fen, and bog, according to trophic classifications in the work of Chee and Vitt [1989]. The bog was a circular, internal collapse scar completely surrounded by frozen peat plateau. The poor and intermediate fens were collapse scars adjacent to peat plateaus. The rich fen was a large unfrozen, minerotrophic peatland typical of the dominant peatlands in northern Manitoba [Halsey *et al.*, 1997]. Within each site, collars were placed along moisture, thermal, plant community, and chemical gradients to capture the full range of environmental conditions (Table 1). Full site descriptions with species composition are found in the work of Bubier *et al.* [1995].

3. Sampling and Measurement Methods

3.1. Method 1, Measurements of ANPP and Soil Respiration

Aboveground net primary productivity (ANPP) was measured for the vascular plant and bryophyte component of each sampling site. Productivity for vascular plants was measured by clipping aboveground vegetation at the end of August before the plants senesced, with three replicate plots

Table 1. Characteristics of Sampling Sites by Wetland Class

Site	Class	Dominant Species	Ph	WT
CB	OlsB	<i>Sphagnum fuscum</i>	3.9	-19.66
		<i>Chamaedaphne calyculata</i>	(0.2)	(2.11)
		<i>Smilacina trifolia</i>		
		<i>Vaccinium oxycoccus</i>		
PF	OgPF	<i>Sphagnum riparium</i>	4.3	-7.69
		<i>Carex aquatilis</i>	(0.1)	(4.98)
		<i>Carex limosa</i>		
IF	OgIF	<i>Sphagnum riparium</i>	5.8	-3.56
		<i>Warnstorfia exannulata</i>	(0.1)	(3.12)
		<i>Carex rostrata</i>		
		<i>Potentilla palustris</i>		
RF	OlsRF	<i>Scorpidium scorpioides</i>	7.2	2.09
		<i>Menyanthes trifoliata</i>	(0.1)	(6.00)
		<i>Andromeda glaucophylla</i>		
		<i>Betula pumila</i>		
		<i>Limprichtia revolvens</i>		

Site codes: CB, collapse bog; PF, poor fen; IF, intermediate fen; RF, rich fen. Classes are O, Open; T, Treed; ts, tall shrub; ls, low shrub; g, graminoid; B, Bog; IF, intermediate fen; PF, poor fen; RF, rich fen. Mean values (standard deviations) for pH, WT (mean water table position in centimeters below peat surface); WT for each site is the average of continuous measurements averaged every hour from May to October, 1996. Site names correspond to the following sites in the works of Bubier *et al.* [1995] and Bellisario *et al.* [1998]: CB = BC (bog collapse scar); PF = FC (fen collapse scar); IF = ZF (Zoltai fen); and RF = TF (tower fen). Also, see Bubier *et al.* [1995, 1997], for CH₄ and CO₂ fluxes, and cation concentrations.

for each site. Clipped vascular plants were sorted into three categories: (1) woody, (2) graminoid (predominantly *Carex* species), and (3) other herbaceous species. The biomass samples were dried at 60°C for 24 to 48 hours and weighed. Woody stem production was estimated at 20% total woody stem biomass [Wallen, 1992]. Bryophyte productivity was measured either by a cranked wire technique [Rochefort *et al.*, 1990] for *Sphagnum* mosses found in the bog and poor fen sites and other mosses with a vertical growth pattern or by Velcro markers for prostrate growth forms, such as "brown" mosses (e.g., *Scorpidium scorpioides*) found in the intermediate and rich fen sites and feather mosses. For each technique, linear increments in growth were measured and converted into mass per unit area using the average bulk density of three replicate 10³ cm³ samples for each species. Bulk density measurements account for stem density differences among species.

Below ground NPP (BNPP) was estimated at 50% of NPP based on Wallen [1992]. BNPP estimated by Wallen ranged from 50 to 80% of NPP; we have chosen the lower estimate because mosses rather than vascular plant dominate NPP at our study sites. Biomass was converted to grams of carbon by using the following ratios: 0.45 for woody biomass and 0.50 for herbaceous biomass [Gower *et al.*, 1997].

Dark CO₂ flux measurements were used to measure total ecosystem respiration. (See Method 3 for chamber techniques). CO₂ flux was measured every week from April

to the end of October 1996. Peat temperature at 5, 10, 20, and 50 cm depth was measured continuously with thermocouples and averaged every hour at each collar location with CR10 and CR7 data loggers (Campbell Scientific, Inc.). An estimate of hourly CO₂ flux from May to October was made using the relationship between CO₂ flux and temperature at 5 cm derived from the observed correlation between weekly respiration measurements and temperature. Correlation coefficients (r^2) for each site ranged from 0.57 to 0.88 ($p < 0.01$). We did several measurements over a 24 hour period to assess differences between daytime and nighttime respiration. We found the relationship between 5 cm temperature and CO₂ flux over the day-night cycle was consistent with that found over the whole season. Winter CO₂ fluxes (November through April) were estimated to be 10% of the April-October flux, based on measurements made in April 1996 at all the sites, and from winter measurements made in Finnish peatlands [Alm *et al.*, 1997].

Autotrophic respiration from roots and aboveground plant components was estimated to be 40% of total ecosystem respiration based on *Silvola et al.* [1996] and *Bhardwaj* [1997]. Heterotrophic respiration (60% of annual CO₂ flux) was subtracted from NPP to derive NEP for each site. Losses of C from DOC and CH₄ flux are not included in the NEP estimates for method 1.

3.2. Method 2, Radiocarbon

Radiocarbon may be used to determine the rates of carbon addition and loss in wetlands during recent decades [Trumbore and Harden, 1997]. Testing of nuclear weapons in the atmosphere in the early 1960s approximately doubled the amount of radiocarbon in atmospheric CO₂. With the cessation of testing in 1964, exchange with ocean and terrestrial carbon reservoirs and burning of ¹⁴C-free fossil fuels has caused a steady decline in atmospheric ¹⁴CO₂. These changes in atmospheric radiocarbon are recorded in plants. Year-to-year changes in ¹⁴C are large enough that the timing of plant growth may be determined to within a year or two over the past 30 years.

To obtain longer-term records of carbon accumulation for analysis using radiocarbon, we collected samples of the upper meter of wetland peat by freeze coring. Freeze coring avoids problems of compaction in the uppermost layers of peat and moss and therefore is more useful for determining bulk density and preserving stratigraphy. A hollow metal rod 1-2 m in length and sharpened at the bottom end was pushed vertically into the peat. Liquid nitrogen was then vented into the hollow tube for 30 to 40 min. Peat frozen to the rod was removed and cut using knives and saws into squares of known volume for bulk density and water content determination. A split of these samples was ground to <100 mesh and analyzed for bulk organic C and N content using a Fisons NA-1500 combustion analyzer. The raw data are available on the BOREAS web site or at the Oak Ridge distributed data archive [Trumbore *et al.*, 1998].

Samples for radiocarbon analysis were cut as slices of roughly 1 to 4 cm vertical thickness from the freeze core. Macrofossils of moss, sedge, or seeds were selected as representative of the time of growth for the plants preserved at a given depth. Roots, which penetrate deeply into peat layers, were avoided because they probably postdate the organic matter matrix in which they grow.

To remove surface contaminants, macrofossils were washed with a mixture of 0.1N sodium hydroxide and 0.1N sodium pyrophosphate, then rinsed with distilled water, 0.5N HCl, and finally distilled water. The samples were dried, sealed in evacuated quartz tubes with CuO wire, and combusted at 900°C for 2 hours. CO₂ evolved during combustion was purified cryogenically and reduced to graphite for measurement by accelerator mass spectrometry (AMS) at the Lawrence Livermore Laboratory Center for AMS. Radiocarbon data are reported in $\Delta^{14}\text{C}$ notation, as the deviation (in parts per thousand) of the ¹⁴C/¹²C ratio of the sample to that of an accepted standard. Samples are corrected to a common $\delta^{13}\text{C}$ of -25‰. Carbon13 analyses were made only on a subset of samples; for the most part we assumed a value of -27‰. A 2‰ error in the value assumed for $\delta^{13}\text{C}$ gives a 4‰ error in the radiocarbon upon correction. The precision of the radiocarbon measurements reported here averaged ± 7 ‰ in $\Delta^{14}\text{C}$.

The year of growth for macrofossils was determined by comparing the measured ¹⁴C value with the time series of ¹⁴C in atmospheric CO₂ since 1963 (see *Trumbore and Harden*, [1997], for details). One potential error in this approach is the possibility that a significant fraction of the carbon fixed by mosses and sedges is derived from respired carbon (which is older and therefore likely higher in ¹⁴C than the atmosphere for a given year since about 1970). Measurements of radiocarbon in living mosses and plants were made in 1995 and 1996 to assess this effect, which was variable but generally not significant.

Addition of carbon occurs both at the peat surface and through root production by vascular plants. Decomposition losses of C occur not only in the upper 1-2 m accessible to the freeze-coring method but throughout the peat column [Clymo, 1984]. To determine the long-term rate of C accumulation in peat and the contribution of decomposition in deeper peat layers to CO₂ loss from each site, we used a modified piston coring device (Livingston corer) to obtain peat cores of up to 4 m depth. We also sampled a frozen section of peat using a permafrost (Sipri) corer on a nearby palsa (frozen peat upland). As with freeze core samples, radiocarbon analyses were made on macrofossils picked from various depth intervals, while bulk density, %C and %N measurements were made on bulk core samples. Negative $\Delta^{14}\text{C}$ values, which indicate that C was fixed prior to 1960, were converted to calendar ages using established calibration curves. These data are reported by *Trumbore and Harden* [1997].

To interpret carbon dynamics from carbon and radiocarbon data, we use a simple first-order model of carbon accumulation and decay. The amount of carbon in a given year ($C(t)$), equals net annual carbon inputs (NPP) minus losses. We assume loss is dominated by decomposition to CO₂ and describe it using a first-order decomposition rate constant, k (units of year⁻¹):

$$dC/dt = \text{NPP} - k C(t). \quad (4)$$

The solution to equation (4) is:

$$C(t) = (\text{NPP}/k) (1 - \exp(-kt)). \quad (5)$$

Time (t) is derived by subtracting the year of plant growth, obtained from radiocarbon, from the year of sampling (1995 or 1996). The amount of carbon accumulated between that

time and the present is determined by summing the carbon inventory (obtained from the bulk density and carbon content measurements) for all sampling intervals above the depth in question. A plot of $C(t)$ versus years before present was then made, and bestfit values for NPP and k determined (Kaleidograph version 3.0). Reported errors for NPP and k are the 95% confidence interval for the curve-fit parameters.

We also attempted to fit curves of C accumulation over the past 35 years using a relation that allows for decomposition rates to decrease linearly with time [Frolking *et al.*, 1996; Harden *et al.*, 1997]. However, the two methods either showed no difference in their ability to fit the data or the formulation with changing decomposition over time failed to fit the data as well as the simpler model (equations (4) and (5)). It is likely that the time span of 35 years is too short for significant changes in k to be discernable.

Our approach determines time from the radiocarbon signature recorded in hand-picked moss and sedge, while bulk density measurements include roots in addition to decomposed mosses and sedges. Hence the values derived for NPP and k are representative of the average of vegetation which may have different times of origin and rates of decay. Our NPP estimate includes both components that probably grew *in situ*, such as mosses and sedges, and those that grew subsequently, such as sedge and shrub roots. By assuming single NPP and k values for bulk organic matter we are implicitly assuming (1) that the rates of decomposition of roots, moss, and leaves are all similar and (2) the depth distribution of roots (i.e., the ratio of root to moss or leaf biomass at any given depth) remains approximately constant in time. If these assumptions hold, we may subtract direct measurements of ANPP from our radiocarbon-derived value for NPP to obtain an estimate of BNPP.

Carbon dynamics change vertically in the peat profile. Carbon input and decomposition rates in the less decomposed organic matter near the surface of the peat are approximately an order of magnitude greater than those of the permanently water-logged and more decomposed underlying layers [Clymo, 1984]. To determine NEP with the radiocarbon method, we need to subtract net respiration of not only the carbon in the upper layers, but also the CO_2 derived from very slow decomposition of the large mass of material that has accumulated since the deglaciation [Clymo, 1984; Tolonen and Turunen, 1996; Turunen and Tolonen, 1996]:

$$\text{NEP} = \text{NPP} - k_{\text{shallow}}C_{\text{shallow}} - k_{\text{deep}}C_{\text{deep}} \quad (6)$$

where k_{shallow} is the decay constant derived from bomb radiocarbon in the upper portion of the peat (normally <70 cm); C_{shallow} is the amount of carbon for which that decomposition constant applies; k_{deep} is the decomposition constant obtained for the deeper peat layers, which is roughly an order of magnitude slower than that obtained for near-surface layers [Trumbore and Harden, 1997], and C_{deep} is the carbon inventory over which the slower decomposition rate applies. The choice of C_{shallow} was made using core descriptions, bulk density, and C/N ratio data. We chose the shallow-deep transition as the depth where peat becomes notably more decomposed, which normally coincided with an increase in bulk density and a shift in C/N ratio. In the poor and intermediate fens, the bomb ^{14}C signature used to determine the NPP and k values extended to greater depths; we chose C_{shallow} in those cases as the depth just below the

1963 growth year (in the case of the intermediate fen this was close to the bottom of the freeze core). Errors were determined by assuming the depth interval chosen was too deep or too shallow by one 4 cm increment for the bog collapse and rich fen; we assumed a larger error of 2 kg C m^{-2} for the poor and intermediate fens to account for uncertainty in the degree of decomposition. The shallow/deep transitions often could not be dated directly using radiocarbon because they fell in the pre-1950 time period, where radiocarbon is not useful on timescales of several hundred years. Input, accumulation and loss rates were determined for nitrogen using the same methods as for carbon.

3.3. Method 3, Net Ecosystem Exchange of CO_2

Net ecosystem CO_2 exchange (NEE) and photosynthetically active radiation (PAR) were measured with a LI-COR 6200 portable photosynthesis system. Whole ecosystem measurements were made with clear, climate-controlled chambers, modeled after a chamber described by Carroll and Crill [1997], designed and constructed at the University of New Hampshire. The chamber walls were constructed of clear Lexan and Teflon film with a removable top to allow equilibration of plant communities to ambient conditions between sampling runs. The climate-control system consisted of a heat exchanger (Dodge Motors transmission cooler) and a cooler to store cold water that was pumped through the heat exchanger. Fans mounted on the inside of the chamber circulated air across the heat exchanger, maintaining the enclosed air within 1°C of outside air temperature. The area of the base of the chambers was 3660 cm^2 ($60 \times 60 \text{ cm}$) to fit a collar with the same area. Chamber heights were either 45 cm or 90 cm to accommodate the varying heights of the vegetation at the different sites.

To establish relationships between NEE and PAR on each sampling day, shrouds with different mesh sizes were used to reduce the light entering the chamber to one half and one quarter full light. An opaque shroud was placed over the chamber to eliminate all light for measuring ecosystem respiration (combined autotrophic and heterotrophic). In each case the chamber was allowed to equilibrate to the new light or dark conditions. Measurements were made within 2 hours either side of solar noon so that the full range of light responses could be measured. Four 2.5 min. sampling runs at different light levels were conducted at each collar location on a weekly basis from mid-April to mid-October 1996. Measurements of PAR and peat temperature were recorded hourly with Campbell Scientific CR10 data loggers. As mentioned above, we made additional measurements of respiration over the 24 hour period several times during the season to ensure that dark respiration values were comparable to nighttime values (corrected for temperature difference). See Bubier *et al.* [1998] for more detail on sampling methods.

A model, using hourly rates of photosynthetically active radiation (PAR) and temperature at 5 cm peat depth, was developed to calculate hourly rates of photosynthesis and respiration and to interpolate between the weekly measurements of CO_2 exchange throughout the entire growing season. Net ecosystem exchange of CO_2 (NEE) is the difference between gross photosynthesis and respiration:

$$\text{NEE} = \frac{mT_{5\text{cm}}}{mT_{\text{seas}}} \times \frac{\alpha \times \text{PAR} \times \text{GP}_{\text{max}}}{\alpha \times \text{PAR} + \text{GP}_{\text{max}}} - 10^{(sT_{5\text{cm}} - 0.1)} \quad (7)$$

Table 2. Estimates of Net Ecosystem Production (NEP) Using Method 1.

	Bog Collapse		Poor Fen		Intermediate Fen		Rich Fen	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
ANPP	80.54	20.32	150.40	39.42	215.00	51.29	144.44	37.96
BNPP	80.54	20.32	150.40	39.42	215.00	51.29	144.44	37.96
NPP	161.08	40.64	300.08	78.84	430.00	102.58	288.88	75.92
HR	163.73	15.50	188.89	21.38	265.85	42.96	273.64	27.46
NEP	-2.65	56.14	111.19	100.22	164.15	145.54	15.24	103.38

Based on aboveground net primary production (ANPP), below ground NPP (BNPP), and heterotrophic respiration (HR) derived from from CO₂ flux data (Method 1). NEP = ANPP + BNPP - HR. Values are all g C m⁻² yr⁻¹. Errors for NEP are calculated as the sum of errors for independent terms. HR is 60% dark CO₂ flux.

The first term imposes a seasonality on the calculated gross photosynthesis rate using a 7 day running average of the peat temperature at 5 cm (mT_{5cm}) divided by the mean seasonal temperature at 5 cm (mT_{seas}). The second term is a rectangular hyperbolic curve fit [Thornley and Johnson, 1990] of gross photosynthesis to PAR. The asymptote, GP_{max} , of the curve fit is the maximum rate of carbon fixation, and α is the initial slope of the curve (also called the apparent quantum yield). Joiner et al. [this issue] found that NEE-PAR relationships for the fen were consistent between morning and afternoon periods. The final term is the respiration response curve determined by the fit of the instantaneous peat temperature at 5 cm (T_{5cm}) to the logarithm of the carbon exchange measured at PAR = 0. The term s in the final exponent is the slope of the respiration-soil temperature relationship. All the data were fit to one equation, instead of separating the data into photosynthesis and respiration, in order to estimate uncertainty in the predicted NEE values.

Uncertainty in the modeled hourly NEE was determined using the Delta method [Arnold, 1990], which is based on a first-order Taylor series approximation of the response function $NEE = h(GP_{max}, \alpha, s)$. See Bubier et al. [this issue] for more details on NEP modeling and uncertainty analysis using NEE measurements. The reported uncertainty is the 95% confidence interval. Net ecosystem production (NEP) was defined as the sum of the hourly NEE values for the entire growing season. Losses of C from dissolved organic carbon (DOC), CH₄ fluxes, and winter CO₂ fluxes were not included in the calculation. Data analyses were performed with the statistical software JMP-IN (SAS Institute, Inc. 1996).

4. Results

4.1. Method 1, Measurements of ANPP and Soil Respiration

The mean (s.d.) NEP for the four sites ranges from -3 (56) g C m⁻² yr⁻¹ in the bog to 164 (145) g C m⁻² yr⁻¹ in the intermediate fen site (Table 2). The bog and rich fen, opposite ends of the ecological gradient, have the lowest NEP values, with the poor and intermediate fens having the greatest. Mean NEP for the bog and rich fen are close to zero, indicating that they could be losing carbon from the ecosystem to the atmosphere. NPP follows the same pattern as NEP with the lowest production in the bog (161 (40) g C

m⁻² yr⁻¹) and highest in the intermediate fen (430 (103) g C m⁻² yr⁻¹). Poor fen and rich fen NPP values are 300 (79) and 289 (76) g C m⁻² yr⁻¹ respectively. Dark CO₂ fluxes follow the ecological gradient bog < poor fen < intermediate fen < rich fen. Heterotrophic respiration ranges from 163 (16) g C m⁻² yr⁻¹ in the bog to 273 (27) g C m⁻² yr⁻¹ in the rich fen. The errors reported for method 1 are standard deviations because we did not always know the number of samples on which literature-derived values were based.

4.2. Method 2, Radiocarbon

Figure 1 plots the ¹⁴C in macrofossils picked from moss and peat layers as a function of depth. The sites with intermediate nutrient status (poor and intermediate fens) have $\Delta^{14}C$ values of +400 ‰ or higher, indicative of C fixed in the early 1960s, at depths of 40-50 cm. The bog and rich fen have shallower ¹⁴C peaks, near 20 cm depth. Peak $\Delta^{14}C$ values from the rich fen site are less than those observed at the other sites. Some 'smearing' of the ¹⁴C signature due to the incorporation of re respired carbon may have occurred in the *Scorpidium* moss that makes up much of this core. We calculated ages assuming a 3 year smoothing of atmospheric radiocarbon values, which is consistent with the ¹⁴C observed for living *Scorpidium* collected in 1995.

Figure 1 also shows the C/N ratio of bulk organic material as a function of depth for the same four sites. C/N ratios follow the trophic gradient, with highest values in the bog and lowest values in the rich fen.

Figure 2 (top) plots carbon accumulation, $C(t)$, versus time for the four wetland sites. NPP and k values obtained from curvefits are given in Table 3. The uncertainties reported are 95% confidence intervals derived from the curve-fitting procedure. The total amount of carbon accumulated over the past 40 years ranges from 2.2 to nearly 11 kg C m⁻², with most carbon at the intermediate and poor fen sites. NPP values are similar for the three fen sites (350-430 g C m⁻² yr⁻¹), and significantly lower at the bog site (161 g C m⁻² yr⁻¹). Decomposition rates cause the large differences in accumulated carbon between fen sites. The fastest decomposition (shortest turnover) rates are at the bog collapse and rich fen, with turnover times of 17-22 years. The intermediate and poor fen sites have turnover times of 42-62 years as determined using radiocarbon.

We also determined the rate of input and decomposition for nitrogen at each site using the same approach (Figure 2

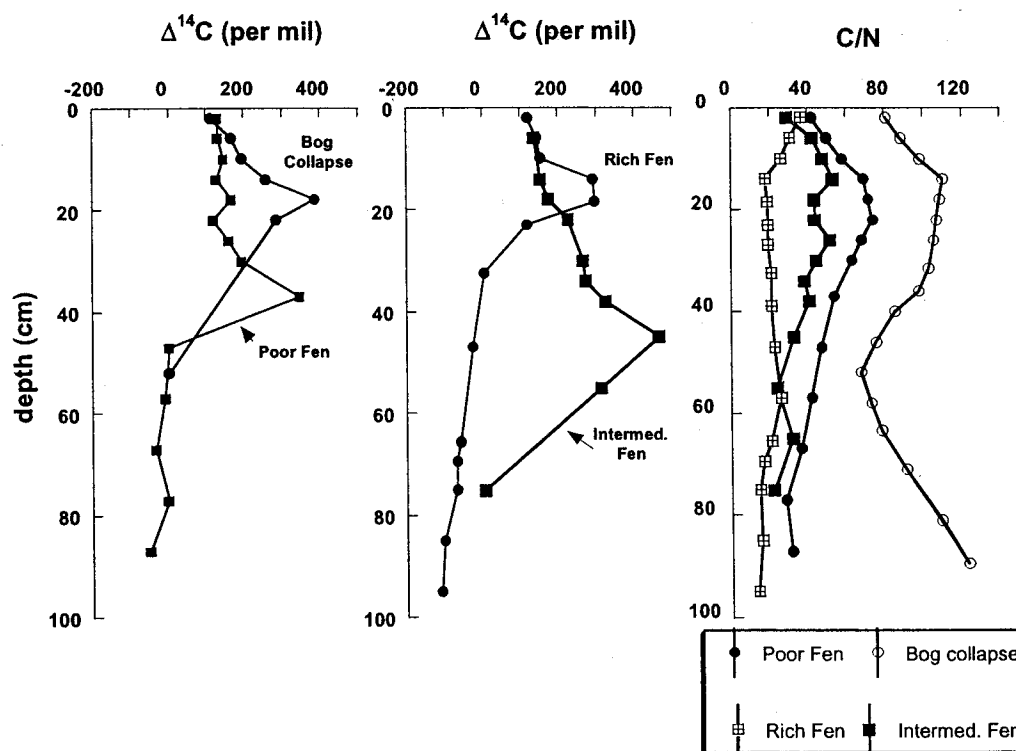


Figure 1. Depth profiles of radiocarbon signature of macrofossils picked from peat and C/N ratio of bulk peat for the four wetland sites. Radiocarbon data are reported as $\Delta^{14}\text{C}$, the per mil deviation of the $^{14}\text{C}/^{12}\text{C}$ ratio from that of a standard (1895 wood).

(bottom) and Table 3). The amount of N accumulated is lower at the bog site compared to the three fens. Annual net N inputs increase with N availability along the trophic gradient, from 1.4 (0.3) $\text{g N m}^{-2} \text{yr}^{-1}$ at the bog to 15.7 (3.3) $\text{g N m}^{-2} \text{yr}^{-1}$

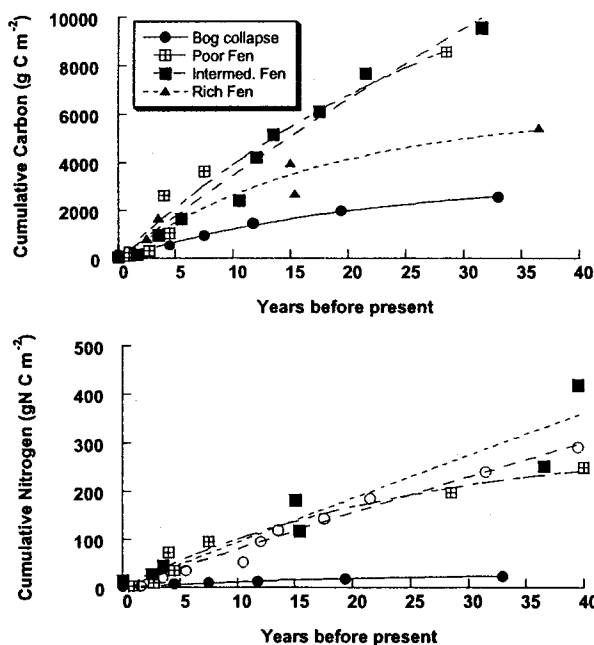


Figure 2. Total amount of carbon (top) and nitrogen (bottom) accumulated versus the age of carbon at the depth above which carbon is inventoried. Ages are derived from comparing the $\Delta^{14}\text{C}$ of peat macrofossils with the time history of ^{14}C in atmospheric CO_2 .

at the rich fen. First-order loss rates for N have similar magnitude and pattern as those derived from C, with faster turnover in the bog and rich fen and slower turnover in the poor and intermediate fens. Turnover times derived using method 2 will mask the dynamics of internal N cycling, since they represent the time for loss of N from the system.

Table 3 also gives the values for other components needed to calculate NEP using the radiocarbon method. The depths used to determine C_{shallow} are 75 cm for the intermediate fen, 50 cm for the poor fen, and 26 cm for both the bog and the rich fen. In deeper peat layers the rates of C input and loss are nearly 10 times less than those found in upper layers. The depth of total peat varied from 2.5 m at the bog collapse to 4.4 m at the rich fen site, with C inventories estimated from bulk density and %C to be 33 kg C m^{-2} at the bog to 192 kg C m^{-2} at the rich fen. Using a k value of $0.0003 \pm 0.0001 \text{ yr}^{-1}$ [Trumbore and Harden, 1997], the $k_{\text{deep}} * C_{\text{deep}}$ term was $10 \pm 3 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the bog collapse and $55 \pm 20 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the rich fen. We did not have deep cores from the intermediate or collapse fen sites with good bulk density data, so we assumed values for $k_{\text{deep}} * C_{\text{deep}}$ of $30 \pm 20 \text{ g C m}^{-2} \text{ yr}^{-1}$ for both.

4.3. Method 3, Direct NEP Measurements

The poor and intermediate fens have greater carbon accumulation over the season than either the bog or the rich fen. NEP for the bog ($3 \pm 9 \text{ g C m}^{-2}$) and rich fen ($13 \pm 24 \text{ g C m}^{-2}$) are near zero, with lower confidence limits below zero, suggesting that both of these ecosystems could be losing carbon on an annual basis. The poor fen ($65 \pm 47 \text{ g C m}^{-2}$) and intermediate fen ($31 \pm 14 \text{ g C m}^{-2}$) have higher NEP, with lower confidence limits above zero. Reported errors are 95% confidence intervals.

Table 3. Input and Decomposition Rates from Method 2

Site	Collapse Bog	Poor Fen	Intermediate Fen	Rich Fen
<i>Carbon Budget</i>				
NPP	150 (10)	430 (80)	380 (40)	340 (80)
<i>k</i> (1/yr)	0.045 (0.008)	0.024 (0.012)	0.016 (0.007)	0.056 (0.024)
TT (yr)	22 (19 – 27)	42 (28 – 83)	61 (43 – 104)	18 (12 – 31)
C_{shallow}	2.6 (0.5)	9.0 (2)	10.8 (2)	4.7 (0.7)
$k_{\text{deep}}C_{\text{deep}}$	10 (3)	30 (20)	30 (20)	55 (20)
NEP	23 (32)	180 (140)	180 (90)	25 (150)
<i>Nitrogen Budget</i>				
N input (\pm)	1.4 (0.3)	6.8 (1.2)	8.0 (0.7)	15.7 (3.3)
<i>k</i> for N (1/yr)	0.05 (0.02)	0.02 (0.014)	0.003 (0.009)	0.05 (0.02)
TT for N (yr)	20 (14 – 33)	50 (34 – 111)	330 (>111)	20 (14 – 32)
Apparent N accumulation	0.3 (0.1)	3.7 (2.0)	7.1 (14)	5.5 (2.5)

Units for C fluxes (NPP, NEP, $k_{\text{deep}}C_{\text{deep}}$) are $\text{g C m}^{-2} \text{yr}^{-1}$ and for N fluxes (input and apparent accumulation) are $\text{g N m}^{-2} \text{yr}^{-1}$. C_{shallow} units are kg C m^{-2} . Values in parentheses are 95% confidence intervals for the curvefits shown in Figure 2. Apparent N accumulation is equal to total N accumulation rate over the past 35 years. If losses of N are zero deeper in the core, this will equal total N accumulation

5. Discussion

5.1 Comparison of Three Methods and Their Uncertainties

NEP values derived using the three approaches are compared in Figure 3. The estimates of NEP show the same magnitude and pattern across the four sites. However, NEP predicted by method 3 is significantly lower at the intermediate fen site.

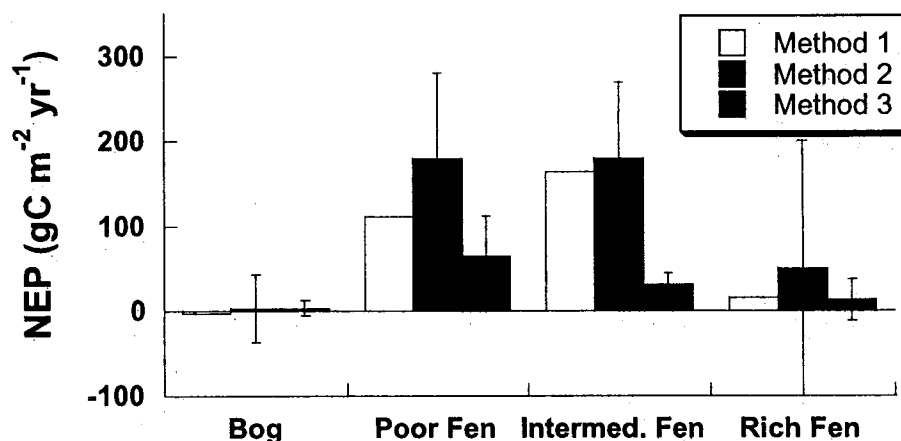


Figure 3. Comparison of net ecosystem production (NEP) estimated using the three methods described in the text.

5.1.1. Method 1. The strength of estimating NEP from measurements of ANPP and soil respiration alone is in its overall simplicity. ANPP may be determined from one-time sampling at the end of the growing season, and components of ANPP may be partitioned among different plant components (sedge, moss, shrub). While soil respiration measurements may be time consuming, the methodology for field sampling is simple. The major weakness is that two very important components, BNPP and the fraction of soil respiration that is heterotrophic, must be estimated from previously published work, often from other locations.

Below-ground production for vascular plant species was estimated to be 50% of total production, at the low end of estimates (which range from 50 to 80% of NPP) for northern peatlands [Wallen, 1986]. Autotrophic respiration was estimated at 40% of total ecosystem respiration. These values are based on studies that were conducted in mid-summer at a time when plant activity is at its maximum. They were also conducted in sites with greater woody plant biomass than at our peatland sites in Manitoba. Winter CO_2 fluxes were estimated to be 10% of those observed in the May-October period. This estimate is higher than that observed by Winston *et al.* [1997] for other BOREAS sites but lower than winter fluxes measured in a Finnish peatland [Alm *et al.*, 1997]. Neither methods 1 or 3 include losses of C from DOC or CH_4 fluxes.

5.1.2. Method 2. A major advantage of the radiocarbon method is that sampling may be a one-time event (coring) rather than labor-intensive campaigns to measure fluxes during the growing season. The estimates of NPP and NEP based on the radiocarbon method represent average rates over the past few decades. Differences in NEP between method 2 and methods 1 and 3, which are both based on a single year of measurements, may be partly explained if NEP was lower in the year measurements were made than the decadal average. A disadvantage to the radiocarbon method is the cost of AMS measurements. It should be noted that other researchers have found cheaper methods for determining long-term average NEP using ^{210}Pb [Turunen and Tolonen, 1996] or identified ash layers [Robinson and Moore, 1999] as chronometers.

The data presented here are for a single core, while data collected for methods 1 and 3 are averaged over a range of sites within each wetland type. Spatial variability in vegetation may be averaged over time in the 35 years

represented by the freeze-coring method. Results for the rich fen are for the portion of that site dominated by *Scorpidium* moss. Other parts of the fen complex are drier and have *Sphagnum* mosses (with higher NEP) instead of brown moss.

5.1.3. Method 3. Direct measurement of NEP offers the opportunity to derive potentially extrapolatable, process-based relationships among NEE, PAR, temperature, and water table at fine temporal resolution. The relationships offer the potential for spatial and temporal scaling and are useful for predicting changes in C accumulation with changes in temperature and moisture balance on seasonal to interannual timescales. The major disadvantage is that chamber methods are labor intensive. In addition, continuous measurements of PAR, temperature, and moisture are needed at each site.

Uncertainties in the interpolation of weekly NEE measurements to derive NEP using hourly measurements of PAR and peat temperature include standard errors in the parameters GP_{max} , α , and s . The uncertainties are greatest at maximum temperatures because the respiration-temperature relationship is a log-linear one [Bubier *et al.*, this issue].

Method 3 has the lowest estimates of NEP in the poor and intermediate fen sites. One explanation for this is that the modeling approach we used underestimates maximum photosynthesis (or GPP) during the summer. The interpolation (equation (7)) uses the seasonal average NEE-PAR relationship and soil temperature to mimic plant physiology. Predicted values are lower than observations for the midseason maximum GP_{max} (in the NEE-PAR relationship) and maximum mid-season soil temperature. Results from the modeling study [Bubier *et al.*, this issue] conclude that mid-season predicted photosynthesis values underestimate measured values by approximately 25%.

5.2. Differences Between Sites

The upper and lower confidence limits of NEP show that the minimum values for the bog and rich fen are negative for all three methods, indicating that these ecosystems could be net sources of carbon to the atmosphere, although over the last several thousands of years they have been net sinks of carbon (3-5 m of peat accumulation). In the dry late summer period of 1994 when water tables fell to 20-30 cm below the peat surface, these two sites were net sources of carbon based on chamber [Bellisario *et al.*, 1998] and tower [Lafleur *et al.*, 1997; Joiner *et al.*, this issue] measurements of net ecosystem exchanges of CO_2 .

The minimum estimates for carbon flux in the poor fen and intermediate fen sites show that they are always net sinks of carbon. Measurements of NEP in 1994 at the same ecosystems showed a similar pattern, with the *Carex*-dominated poor and intermediate fens having the highest carbon accumulation rates, as compared with the bog and rich fen [Bellisario *et al.*, 1998]. In that study, aboveground sedge biomass was correlated with NEP, suggesting that *Carex* species are highly productive vascular plants. Alm *et al.* [1997] also found that *Carex* sites had the highest growing season NEP compared with hummocks, saturated flarks, and *Eriophorum* lawns in Finnish bog sites.

In northern Manitoba, *Carex*-dominated poor and intermediate fens are often associated with the collapse of frozen peat plateaus, which could have implications for long-term climate change and melting of permafrost. Camill and Clark [1997] found that *Carex*-dominated collapse scars were

of recent origin compared with *Sphagnum fuscum*-dominated internal collapse scars. In our study, the *Sphagnum fuscum* bog collapse scar was accumulating less carbon than the *Carex*-dominated poor and intermediate fen collapses. If the latter peatlands are younger collapse features than the bog collapse, it would suggest that carbon accumulates rapidly in the early stages of permafrost degradation, then slows to a lower rate in more stable ecosystems. Other studies that have shown faster C accumulation in younger ecosystems include Turunen and Tolonen [1996]. Halsey *et al.* [1997] reported a correlation between distribution of permafrost collapse scars and mean annual temperature, but the development of these features may also have local mediating influences, such as disturbance and vegetation dynamics [Camill and Clark, 1997].

NPP is similar at the three fen sites. Therefore, higher C accumulation rates at the poor and intermediate fen must be due to slower overall decomposition rates. Large numbers of sedge roots are present at the poor and intermediate fen sites, and a larger portion of NPP is allocated belowground at *Carex*-dominated sites (see below). Data from an in situ wetland decomposition experiment shows that sedge roots decompose more slowly than other plant tissue [Moore *et al.*, 1999]. At the poor and intermediate fen sites, roots may be dominating the decomposition rate obtained from ^{14}C . While other studies have found faster decomposition at rich fens than more nutrient-poor fens [Malmer, 1986], this is counter to observations of slower decomposition in bogs than fens made in the same studies. At the collapse bog site, the average depth to the water table is greater than at the other sites (Table 1). A larger aerobic zone may lead to faster decomposition rates.

Heterotrophic respiration as calculated from method 2 (radiocarbon; equal to $k_{shallow}C_{shallow} + k_{deep}C_{deep}$) ranges from 46 to 78% (average $60 \pm 14\%$) of total dark respiration measured at each site (Table 1). This is in accord with the literature-based estimate of 60% heterotrophic respiration used in method 1. Respiration rates are lowest at the bog collapse even though decomposition rates are fast because of overall lower productivity.

The apparent rate of annual N accumulation calculated in Table 3 ranges from $0.3 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the bog up to $3\text{-}7 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the fens. The rate of N accumulation in the bog, which should derive its N mostly from atmospheric N inputs, is close to estimated atmospheric N deposition rates (0.2 to $0.3 \text{ g N m}^{-2} \text{ yr}^{-1}$). However, the annual amount of N added as fresh plant residues is significantly larger ($1.4 \text{ g N m}^{-2} \text{ yr}^{-1}$). If new N inputs are derived from the atmosphere, this difference would indicate that ~80% of the N taken up by plants annually comes from decomposition of plant residues.

5.3. Calculation of BNPP From ANPP and NPP by Combining Methods

If we assume the NPP values obtained using the radiocarbon method are correct, we may obtain an estimate of belowground production by subtracting the measured values of ANPP (method 1). Figure 4 shows the breakdown on ANPP into woody, sedge plus herb, and moss components. At all sites, moss is the largest portion of ANPP, with sedges and herbs contributing the most to vascular plant ANPP at the poor and intermediate fen sites. The total NPP calculated using method 1 (assuming ANPP and BNPP are both 50% of

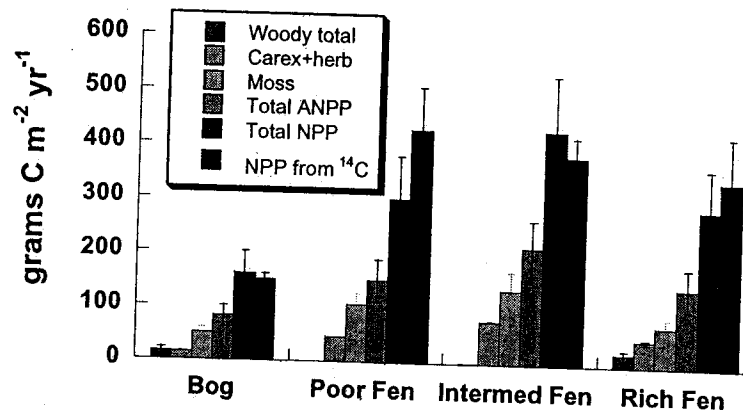


Figure 4. Comparison of estimates of net primary production (NPP) using methods 1 and 2. The breakdown of above-ground net primary production (ANPP) into different components is shown. Total NPP is calculated in method 1 assuming that below-ground production is 50% of ANPP. This value compares favorably with the NPP derived from method 2 (NPP from ¹⁴C) except for the poor fen.

NPP) is comparable to that obtained from method 2. Within stated errors, NPP values are the same for both methods across sites, which indicates the assumption of $BNPP=ANPP$ made in method 1 is likely reasonable. The implied $BNPP/NPP$ ratio derived by subtracting measured ANPP (method 1) from total NPP (method 2) ranges from 0.39 to 0.93, with the highest value at the poor fen site. Since ~50-70% of the ANPP is in mosses, the woody and sedge/herb plants must allocate a significant portion of their production belowground. Saarinen [1996] found that roots of *Carex rostrata* (the species found at our intermediate fen site) penetrated deep into peat (230 cm) and accounted for 74% of total production.

6. Conclusions

Three independent methods yield the same magnitude and pattern of NEP at four wetland sites along a trophic gradient in the BOREAS northern study area. Carbon accumulation rates were greatest at the intermediate and poor fen sites, largely due to slower decomposition rates of C in the upper layers of peat. Carbon accumulation rates were near zero for both a bog (low inputs matched by low outputs) and a rich fen (high productivity and respiration).

Each method used to determine NEP has significant advantages, disadvantages, and sources of uncertainty. The use of more than one method allows for estimation of parameters that are difficult to measure directly, such as the fraction of NPP that is belowground (BNPP) and the fraction of total respiration that is heterotrophic (HR). Because the measurements being compared represent different timescales of averaging (days to months for methods 1 and 3, decades to millennia for method 2), these comparisons must be made cautiously.

Decadal-average nitrogen inputs, losses, and accumulation were also estimated using method 2. Fens accumulate N at least 10 times faster than the bog, which was accumulating N at approximately the same rate as the supply from the atmosphere.

Acknowledgments. We thank R. Varner, A. Mosedale, C. Mosedale, K. Savage, S. Mifflin, T. Black, D. Maher, S. Zheng and A. Hirsch for superb assistance in the field and laboratory; D. Peteet

for assistance in coring; NASA staff for support during the BOREAS experiment; NASA grants to S. Trumbore, J. Harden, and P. Crill; a DOE Global Change Postdoctoral Fellowship to J. Bubier. The U.S. Geological Survey Carbon Cycle Program provided additional support for J.W. Harden, as well as funds for development of the freeze-coring method.

References

- Alm, J., A. Talanov, S. Saarnio, J. Silvola, E. Ikkonen, H. Aaltonen, H. Nykanen, and P. J. Martikainen, Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland, *Oecologia*, 110, 423-431, 1997.
- Arnold, S.F., *Mathematical Statistics*, Prentice Hall, Englewood Cliffs, N. J., 1990.
- Bellisario, L., T. R. Moore, and J. L. Bubier, Net ecosystem CO₂ exchange in a boreal peatland, northern Manitoba, *Ecoscience*, 5, 534-541, 1998.
- Bhardwaj, A., *Seasonal Variability of Net Carbon Dioxide Exchange in a Headwater Bog, Kenora, Ontario*, Geog. Dept., McGill Univ., Montreal, Que., 1997.
- Bubier, J.L., T.R. Moore, L. Bellisario, N.T. Comer, and P.M. Crill, Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, *Global Biogeochem. Cycles*, 9, 455-470, 1995.
- Bubier, J.L., P.M. Crill, T.R. Moore, K. Savage, and R.K. Varner, Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex, *Global Biogeochem. Cycles*, 12, 703-714, 1998.
- Bubier, J.L., S. Frohling, P.M. Crill, and E. Linder, Net ecosystem productivity and its uncertainty in a diverse boreal peatland, *J. Geophys. Res.*, this issue.
- Camill, P., and J.S. Clark, Climate change disequilibrium of boreal permafrost peatlands caused by local processes, *Am. Nat.*, 151, 207-222, 1997.
- Carroll, P., and P.M. Crill, Carbon balance of a temperate poor fen, *Global Biogeochem. Cycles*, 11, 349-356, 1997.
- Chee, W.-L., and D. H. Vitt, Vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada, *Wetlands*, 9, 227-261, 1989.
- Clymo, R.S., The limits to peat bog growth, *Philos. Trans. R. Soc. London*, 303, 605-654, 1984.
- Frohling, S., et al., Modeling temporal variability in the carbon balance of a spruce/moss boreal forest, *Global Change Biol.*, 2, 343-366, 1996.
- Gorham, E., Northern peatlands: Role in the carbon cycle and probable responses to climatic warming, *Ecol. Appl.*, 1, 182-195, 1991.
- Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, S.J. Steele, and T.K. Stow, Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in

- Saskatchewan and Manitoba, Canada, *J. Geophys. Res.*, 102, 29,029-29,041, 1997.
- Halsey, L., D. Vitt, and S. Zoltai, Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada, *Wetlands*, 17, 243-262, 1997.
- Harden, J. W., E. T. Sundquist, R. F. Stallard, and R. K. Mark, Dynamics of soil carbon during deglaciation of the Laurentide Ice Sheet, *Science*, 258, 1921-1924, 1992.
- Harden, J. W., K. P. O'Neill, S. E. Trumbore, H. Veldhuis, and B. J. Stocks, Moss and soil contributions to the annual net carbon flux in a maturing boreal forest. *J. Geophys. Res.*, 102, 28,817-28,830, 1997.
- Joiner, D.W., P.M. Lafluer, J.H. McCaughey, and P.B. Bartlett, Interannual variability in carbon dioxide exchanges at a northern boreal wetland in the BOREAS northern study area, *J. Geophys. Res.* this issue.
- Lafluer, P. M., J. H. McCaughey, D. W. Joiner, P.A. Bartlett, and D. E. Jelinski, Seasonal trends in energy, water and carbon dioxide fluxes at a northern boreal wetland, *J. Geophys. Res.*, 102, 29,009-29,020, 1997.
- Malmer, N., Vegetational gradients in relation to environmental conditions in northwestern European mires, *Can. J. Bot.*, 64, 375-383, 1986.
- Rapalee, G., S. E. Trumbore, E. A. Davidson, J. W. Harden, and H. Veldhuis, Scaling soil C stocks and fluxes in a boreal forest landscape, *Global Biogeochem. Cycles*, 12, 687-701, 1998.
- Robinson, S.D., and T.L. Moore, Carbon and peat accumulation over the past 1200 years in a landscape with discontinuous permafrost, northwestern Canada, *Global Biogeochem. Cycles*, 13, 591-602, 1999.
- Rochefort, L., D. H. Vitt, and S. E. Bayley, Growth, production, and decomposition dynamics of Sphagnum under natural and experimentally acidified conditions, *Ecology*, 71, 1986-2000, 1990.
- Saarinen, T., Biomass and production of two vascular plants in a boreal mesotrophic fen, *Can. J. Bot.*, 74, 934-938, 1996.
- Schlesinger, W. H., *Biogeochemistry: An Analysis of Global Change*, Academic, San Diego, Calif., 1996.
- Silvola, J., J. Alm, U. Ahlholm, H. Nykanen, and P. J. Martikainen, The contribution of plant roots to CO₂ fluxes from organic soils, *Biol. Fert. Soils*, 23, 126-131, 1996.
- Teller, J. T., and L. Clayton (eds.), *Glacial Lake Agassiz*, 451 pp., Geol. Assoc. of Can., Dep. of Geol., Mem. Univ. of Newfoundland, St. John's, Canada, 1983.
- Thornley, J. H. M. and I. R. Johnson, *Plant and Crop Modeling: A Mathematical Approach to Plant and Crop Physiology*, Clarendon, Oxford, England, 1990.
- Tolonen, K., and J. Turunen, Accumulation rates of carbon in mires in Finland and implications for climate change, *Holocene*, 6, 171-178, 1996.
- Trumbore, S. E. and J. Harden, Accumulation and turnover of carbon in soils in the BOREAS NSA: 1. Methods for determining soil C balance in surface and deep soil, *J. Geophys. Res.*, 102, 28,805-28,816, 1997.
- Trumbore, S. E., J. W. Harden, E. Sundquist and S. K. Conrad, BOREAS TGB-12 soil carbon data over the NSA data set, <http://www-eosids.ornl.gov/>, Distrib. Active Arch. Cent., Oak Ridge Natl. Lab, Oak Ridge, Tenn., 1998.
- Turunen, J., and K. Tolonen, Rate of carbon accumulation in boreal peatlands and climate change, in *Global Peat Resources*, edited by E. Lappalainen, pp. 21-28, Int. Peat Soc., Jyska, Finland, 1996.
- Vitt, D. H., L. A. Halsey and S. C. Zoltai, The bog landforms of continental western Canada in relation to climate and permafrost patterns, *Arc Alp. Res.*, 26, 1-13, 1994.
- Wallen, B., Above and below ground dry mass of three main vascular plants on hummocks on a subarctic peat bog, *Oikos*, 46, 51-56, 1986.
- Wallen, B., Methods for studying below-ground production in mire ecosystems, *Suo*, 43, 155-162, 1992.
- Winston, G., E. T. Sundquist, B. B. Stephen and S. E. Trumbore, Winter CO₂ fluxes in a boreal forest, *J. Geophys. Res.*, 102, 28,795-28,804, 1997.
- Zoltai, S. C., Wetland environments and classification in *Wetlands of Canada*, pp. 3-26, Polysci. Publ., Inc., Montreal, Que., Canada, 1988.
- Zoltai, S. C., Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada, *Arct. Alp. Res.*, 25, 240-246, 1993.
- J. L. Bubier, Environmental Studies Program, Mt. Holyoke College, 50 College Street, So. Hadley, MA 001075. (jbubier@mtholyoke.edu)
- P. M. Crill, Complex Systems Research Center, University of New Hampshire, Durham, NH 03824 (patrick.crill@unh.edu)
- J. W. Harden, U.S. Geological Survey, 345 Middlefield Road, Menlo Park, CA 94025. (jharden@usgs.gov)
- S. E. Trumbore, Department of Earth System Science, University of California, Irvine, CA 92697-3100. (setrumbo@uci.edu)

(Received October 5, 1998; revised March 23, 1999; accepted June 2, 1999.)