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Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area

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Abstract. Rates of input, accumulation, and turnover of C differ markedly within soil profiles and in soils with different drainage in the BOREAS northern study area. Soil C storage increases from ~3 kg C m^{-2} in well-drained, sandy soils to greater than 100 kg C m^{-2} in wetlands. Two modes of C accumulation were observed in upland soil profiles. Large annual C inputs (0.06–0.1 kg C m^{-2} yr^{-1}) and slow decomposition (turnover times of 6–250 years) lead to rapid C accumulation in regrowing surface moss and detrital layers following fire. Deep organic layers that have accumulated over the millennia since the initiation of soil development, and are located below the most recent charred horizon, show slower rates of input (0.015–0.03 kg C m^{-2} yr^{-1}) and turnover (100–1600 years) and accumulate C about 10 times slower than surface detrital layers. Rates of C input to soils derived from C and ^{14}C data were in accord with net primary production estimates, with highest rates of input (0.14–0.6 kg C m^{-2} yr^{-1}) in wetlands. Turnover times for C in surface detrital layers were 6–15 years for well-drained sand soils that showed highest soil temperatures in summer, 30–40 years for wetlands, and 36–250 years for uplands with thick moss cover and black spruce trees. Long (>100 years) turnover times in upland black spruce/clay soils most likely reflect the influence of woody debris incorporated into detrital layers. Turnover times for deep organic and mineral layer C were controlled by drainage, with fastest turnover (80–130 years) in well-drained sand soils and slowest turnover (>3000 years) in wetlands. Total C accumulation rates, which account for C losses from both deep organic and surface detrital layers, are close to zero for sand/jack pine soils, 0.003–0.01 kg C m^{-2} yr^{-1} for moderately to poorly drained sites in mature forest stands, and 0.03 kg C m^{-2} yr^{-1} for a productive fen. Decomposition of organic matter more than several decades old accounts for 9–22% of total heterotrophic respiration at these sites. The rates of C accumulation derived here are decadal averages for specific stands and will vary as stands age or undergo disturbance. Extrapolation to larger regions and longer timescales, where burning offsets C gains in moss layers, will yield smaller rates of C storage.

1. Introduction

Soil organic matter is an important component of the carbon budget in boreal forests [*Gorham*, 1991; *Post et al.*, 1982; *Tolonen and Turunen*, 1996; *Tolonen et al.*, 1992]. The estimated amount of C stored in boreal peatlands alone is 190–550 Pg C [*Gorham*, 1991]. Upland forest soils contain an additional ~12–13% of the 1500 Pg C stored globally in nonpeatland soils [*Post et al.*, 1982]. Living biomass stores of C range from less than 4% of soil C in peatlands [*Gorham*, 1991] to >100% of soil C stocks in upland boreal forests [*Bonan*, 1990]. The large stores of C in boreal soils accumulated since the retreat of the Laurentide ice sheet [*Harden et al.*, 1992], and accumulation in peatlands continues today [*Clymo*, 1984; *Goreham*, 1991].

Fire episodically burns carbon in upland soils and decouples C dynamics averaged over millennial timescales from C accumulation between fires. Sequestering of C in regrowing trees and mosses [*Dyrness and Norum*, 1983] is an obvious component of recent C dynamics on decadal timescales. Moss layer thickness and C inventory increase with time since the last fire, and thick mats of dead moss and roots (up to ~40 cm deep) are found in mature stands of black spruce. Fire recurrence intervals in the northern boreal zone average about 100 years [*Kasischke et al.*, 1995; *Stocks*, 1993].

An important issue is whether present rates of C accumulation in boreal ecosystems may be larger than they have been in the past. Increases in primary productivity in boreal forests caused by increased deposition of N [*Schindler and Bayley*, 1993; *Townsend et al.*, 1996], changing climate [*Darrigo and Jacoby*, 1993], or changes in disturbance frequency [*Kurz et al.*, 1995] could potentially store CO_2 as increased stocks of biomass and soil organic matter. If decomposition rates are slow, many decades may be required before increased respiration significantly offsets higher C inputs. In the intervening time, the system will act as a net C sink. Thus an assessment of the turnover time of soil carbon is required to determine for how long and to what degree increased productivity in boreal forests may lead to a carbon sink [*Thompson et al.*, 1996]. Conversely, increased decomposition rates in these C-rich soils

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may result from future temperature increases [*Moore and Knowles*, 1990], resulting in a potentially large net C source to the atmosphere.

This paper discusses differences in C inputs, storage, and turnover over the range of vegetation/soil types found at the BOREAS northern study area (NSA) [*Sellers et al.*, 1995]. We use radiocarbon as the major tool for quantifying the balance of inputs and decomposition and apply methods used to quantify C balance in wetlands [*Clymo*, 1984; *Gorham*, 1991; *Tolonen and Turunen*, 1996; *Tolonen et al.*, 1992; *Turunen and Tolonen*, 1996] to upland soils. Natural radiocarbon is used to determine rates of C input and turnover in organic layers and mineral soil on millennial timescales. The incorporation of ^{14}C produced by atmospheric nuclear weapons testing (bomb ^{14}C) into surface detritus and moss layers, together with the amount of C sequestered since the last fire event, are used to constrain the balance of C over the past several decades. By resolving total carbon accumulation into the balance of short- and long-term-averaged inputs and decomposition, we can determine whether soils are in C balance on average in the 1990s, assess the contribution of C from slowly decaying organic matter in organic and mineral soil layers to the overall annual heterotrophic respiration by soils, and hypothesize ways in which C balance for a given year may deviate from decadal- or millennial-average rates.

Sites and Sampling Approach

The BOREAS northern study area (NSA), located near Thompson, Manitoba, is near the northern limit of closed-crown boreal forests in Canada. Vegetation is predominantly black spruce (*Picea mariana*) stands of varying density, developed on soil derived from glacial Lake Agassiz sediments. Permafrost underlies much of the upland clay soil; collapse features underlie bogs and wetter areas. Relief is generally low with abundant wetlands. Kame deposits of sand and gravel make up the higher elevation areas, which have predominantly jack pine vegetation (*Pinus banksiana*). Detailed information on sites may be found elsewhere in this volume and in the work of *Sellers et al.* [1995].

We stratified soil sampling to include the two dominant landscape features controlling vegetation and soil C storage: soil drainage and time since the last stand-killing fire. We identified four major drainage classes: (1) well-drained soils with sand and gravel parent material and jack pine vegetation (NSA young jack pine (YJP) burned in 1964) and old jack pine (OJP) flux tower sites); (2) moderately drained soils developed on lacustrine clay, with feathermoss (*Pleurozium/Hylocomium*) the dominant soil cover and with dense stands of black spruce (NSA old black spruce (OBS) site and auxiliary sites burned in 1956 (SOBA) and 1964 (GR)); (3) poorly drained soils on clay with sphagnum moss cover and sparse, stunted black spruce stands (NSA OBS site and auxiliary sites burned in 1956 and 1964); and (4) wetlands (including bogs and fens near the NSA fen flux tower site described by *Bubier et al.* [1995]). To decipher the dynamics of moss regrowth after fire, we selected a series of sites that differed in the time since the last stand-killing fire (for details, see *Harden et al.* [this issue]. A subset of these samples were used for radiocarbon analyses.

Several distinct classes of organic matter are present in boreal forest soils: vascular plant detritus, including roots, woody debris, and conifer needles; living and slightly decomposed (but still recognizable) mosses; black, humified organics and charcoal; mineral-associated organic matter; and C inherited from lacustrine clay parent material. For discussion of C dynamics we divide the soil into two components: surface detritus and deep organic layers plus mineral soil. Surface detritus includes not only vascular plant litter but also living mosses and accumulated mats of dead moss and roots. We defined the top of this layer as the living moss surface and the base as the top of either a charred layer or mineral soil. Feather mosses (*Pleurozium*, *Hylocomium*), brown mosses (e.g., *Scorpidium*), and sphagnum mosses are significant components of ecosystem productivity and metabolic respiration in wetlands and in black spruce stands underlain by permafrost [*Oechel and Van Cleve*, 1986]. Deep organic layers are located at the base of surface detrital layers and include more decomposed organic matter as well as charred material. These layers have higher bulk density and darker color than overlying, relatively undecomposed detrital material. Deep organic layers may be thin or intermittent in moderately to well-drained upland soils. Mineral-associated organic matter is included with deep organic layers for A horizons of clay soils. In soils developed on sand parent material, significant stores of organic matter are present in Bh or Bs horizons, which are designated here as deep organic carbon. In wetlands we arbitrarily distinguished a surface layer, which has C fixed in the last 30 years as identified by ^{14}C content, and a deep organic layer that extends to the mineral soil.

Methods

Field and Laboratory Measurements

Methods of field sampling, determination of bulk density, and soil water content are described in a companion paper [*Harden et al.*, this issue]. Percent C and N of bulk organic material ground to <100 mesh were determined by using a Fisons NA1500 combustion analyzer. Data for C inventory and radiocarbon for all soils sampled are available through the BORIS data archive (TGB-12). We selected a subset of soil profiles for radiocarbon analysis that represented the range of soil drainage (in uplands) and nutrient status (in wetlands) to span the range of variability across the NSA landscape.

Radiocarbon measurements of organic matter were made by accelerator mass spectrometry (AMS) according to methods described by *Trumbore et al.* [1995]. Organic matter from soils was combusted at 900°C in evacuated, sealed quartz tubes in the presence of cupric oxide wire [*Buchanan and Corcoran*, 1959]. The resulting CO_2 was cryogenically purified, then converted to graphite targets for AMS using the zinc reduction method described by *Vogel* [1992]. Radiocarbon data are reported as $\Delta^{14}C$, the per mil deviation of the $^{14}C/^{12}C$ ratio in the sample from that of an oxalic acid standard that has been decay corrected to 1950 [*Stuiver and Polach*, 1977]. The reported ^{14}C data have also been corrected for mass-dependent fractionation effects, using an assumed $\delta^{13}C$ value of $-25‰$ for all samples. Using this notation, positive values of $\Delta^{14}C$ indicate the presence of bomb-produced ^{14}C, and negative values indicate the predominance of C fixed from the atmosphere long enough ago for significant radioactive decay of ^{14}C (half-life = 5730 years) to have occurred. The analytical uncertainty for determination of ^{14}C for graphite targets prepared in our laboratory averages $\pm 8‰$ for samples containing bomb ^{14}C, based on repeated measurements of secondary standards.

Samples analyzed for radiocarbon included specific, identifiable, plant macrofossils in addition to bulk, homogenized organic and mineral layer samples. For example, sphagnum mosses grow upward in a regular manner, so that the record of ^{14}C in atmospheric CO_2 over the past 30 years may be easily seen in a depth profile in the thick moss layers (see discussion below). To construct accumulation rates of mosses through time and to exclude the confounding influences of living roots that penetrate deep into mosses, we picked individual moss leaves and stems for ^{14}C analyses from undried moss samples. These were rinsed in distilled water and dilute HCl in an ultrasonic bath to remove soluble organic matter and fine roots. For the brown moss and sedge fen, both moss and sedge macrofossils were picked and cleaned for ^{14}C analysis. For feather mosses and lichens growing on drier sites we measured the ^{14}C content of bulk material, which included fine roots and aboveground litter from trees and shrubs. In both cases we model the dynamics of moss-dominated layers assuming non-moss components act similarly with respect to accumulation and decay.

Radiocarbon measurements of highly decomposed deep organic layers and mineral soil horizons were made on homogenized bulk samples ground to <100 mesh. Some mineral horizons contained significant quantities of calcium carbonate; this was removed prior to measurement of ^{14}C in organic matter using dilute HCl. Carbon in deep organic layers had $\Delta^{14}C$ values less than 0‰, indicating that most of the carbon in those layers was fixed from the atmosphere more than a century ago.

Determination of C Balance in Surface Organic Layers

We used several methods to quantify the dynamics of C in surface detrital layers. A basic assumption underlying all methods is that the net change in C storage (dC/dt) represents the balance between annual C inputs (I; kg C m^{-2} yr^{-1}) and decomposition (kC, where k is a first-order decomposition rate constant (year^{-1}) and $C(t)$ is the organic layer C inventory kg C m^{-2}) in year t. The C balance for any given year is [*Clymo*, 1984; *Harden et al.*, this issue; *Harden et al.*, 1992]

$$dC/dt = I - kC(t) \tag{1}$$

Solving this equation yields

$$C(t) = (I/k)*(1 - \exp(-kt)) \tag{2}$$

Radiocarbon data may be used in two ways to estimate input and decomposition rates. The first method, used at all sites, applies a simple model of C accumulation to determine I and k values that reproduce observed total C inventory and inventory-weighted mean ^{14}C content in detrital layers accumulated since the last fire or since the drying of glacial Lake Agassiz (or, for wetlands, since ~1960). For a subset of the sites where surface detrital layers are dominated by sphagnum moss, vertical mixing of moss and detrital layers is minimal. In such cases, radiocarbon data may be used to determine the age of C at a given depth. A plot of accumulated carbon inventory ($C(t)$) versus the time it took to accumulate (t, from radiocarbon) may then be fit with (2) to derive estimates of I and k describing either decadal (bomb radiocarbon) or millennial (natural radiocarbon) C dynamics.

A third method for determining I and k values is presented in a companion paper [*Harden et al.*, this issue]. Equation (2) is fit to a plot of mean detritus/moss C inventory across sites that differ in the time since the last stand-killing fire (t). In this paper, we compare I and k values derived by using the accumulation, ^{14}C age, and chronosequence model approaches for soils with different drainage.

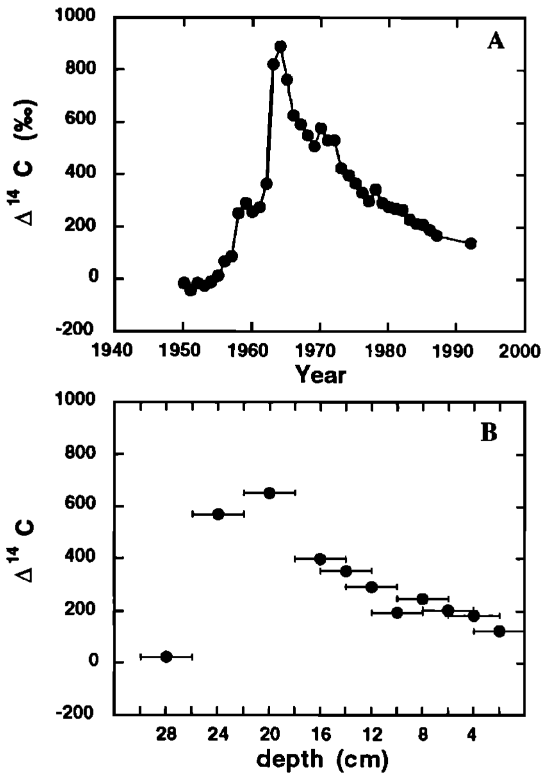

Figure 1. (a) Radiocarbon record of CO_2 atmosphere since 1950; data are from *Burcholadze et al.* [1989] and our own measurements of atmospheric ^{14}C since 1992; (b) $\Delta^{14}C$ values for *Sphagnum fuscum* leaves with depth at the Gillam Road 1964 control site (GR4 in Tables 1 and 2). Error bars represent the depth integrated for each sample. The time since initial C fixation (the age) of sphagnum at any depth is determined by comparison with the atmospheric ^{14}C record.

Equations (1) and (2) imply that C inventory in surface moss and detritus is zero immediately after a fire and that I and k remain constant as detrital layers regrow. Other approaches to modeling decomposition assume that k changes with time [*Clymo*, 1984; *Frolking et al.*, 1996]. Our purpose here is to contrast rates of C input and decomposition over the past several decades with those on millennial timescales and to determine how these factors vary across the landscape. Linking these two timescales requires an understanding of why a shift in decomposition rates occurs. If the reason for the difference in decadal and millennial decomposition rates is disturbance (such as fire) or the movement of material below the oxic/anoxic interface in wetlands [*Clymo*, 1984], forcing the decomposition rate to be a continuous function of time may not be the most appropriate parameterization.

Accumulation Model: All Sites

Because of the large changes in atmospheric ^{14}C content since the late 1950s, the input function for radiocarbon in moss layers differs from the constant input rate assumed for carbon in (1) and (2). Figure 1a shows the record of ^{14}C in northern hemisphere atmospheric CO_2 as recorded in Georgian wines [*Burcholadze et al.*, 1989]. Radiocarbon values in CO_2 peaked in the northern hemisphere (where bomb tests were mostly

Table 1. Summary of Input and Decomposition Rates for Surface Detrital and Moss Layers From ^{14}C Models

Site	Fire Age	Total C	Recent C	$\Delta^{14}C$ (‰)	Recent/Total	I (±)	k	$I - kC_{surf}$
			Well-Drained Sand With Jack Pine and Lichen					
Young jack pine (YJP1)	30	1.9	0.2	+173	0.11	0.03	0.17	0.005
Young jack pine (YJPK1)	30	1.7	0.4	+174	0.24	0.08	0.17	0.014
Young jack pine (YJPK2)	30	···	0.5	+231	···	0.08	0.08	0.006
Old jack pine (OJP1)	80–100	2.9	1.1	+238	0.38	0.06	0.07	0.004
			Moderately Well Drained Clay + Feather Moss					
Gillam Road (GR1)	30	9.3	0.7	+120	0.08	ND	ND	ND
Gillam Road (GR2)	30	11.9	0.9	+206	0.08	ND	ND	ND
Soab River (SOAB3)	38	···	1.4	+238	···	ND	ND	ND
Soab River (SOAB8)	38	···	3.6	+85	···	ND	ND	ND
Soab River (SOAB12)	38	4.7	0.5	+111	0.10	ND	ND	ND
Old black spruce (OBSP11)	117	4.3	1.3	+192	0.30	0.04	0.025	0.003
Old black spruce (OBSP6)	117	···	8.7	+121	···	0.11	0.007	0.048
Old black spruce (OBSP8)	117	···	5.3	+122	···	0.07	0.006	0.031
Old black spruce (OBSF3)	117	···	2.7	+108	···	0.03	0.003	0.021
Old black spruce (OBSF4)	117	···	5.8	+163	···	0.11	0.015	0.020
			Poorly Drained Clay + Sphagnum					
S. fuscum (GR3)	30	18.7	2.2	+262	0.12	0.15	0.05	0.040
(from Figure 3)						0.10 (0.04)	0.0001 (0.04)	0.100
S. warnstorfii (GR4)	110	16.8	4.6–5.4	163–206	0.27–0.32	0.10–0.11	0.016–0.023	0.009–0.016
(from Figure 3)						0.087 (0.016)	0.014 (0.011)	
S. warnstorfii (OBSP9)	117	27.9	8.8–10.3	170–200	0.31–0.37	0.22–0.25	0.019–0.027	0.02–0.05
(from Figure 3)						0.11 (0.02)	0.018 (0.017)	
			Wetlands					
Tower fen (*Scorpidium*)	···	78–120	5.2	+200	0.04–0.07	0.15	0.024	0.026
Tower fen (*S. warnstorfii*)	···	···	6.7	+290	···	0.35	0.031	0.15
(from Figure 3)						0.34 (0.02)	0.029 (0.005)	
Fen collapse (*S. riparium*)	···	···	11.7	+300	···	0.6	0.029	0.26
(from Figure 3)						0.57 (0.08)	0.042 (0.011)	
Bog collapse (*S. fuscum*)	···	···	2.3	+257	···	0.17	0.058	0.04
(from Figure 3)						0.14 (0.02)	0.045 (0.013)	

Total C is C inventory integrated over the depth to mineral horizons with $CaCO_3$ (in upland clay soils) or the base of Bs horizons in well-drained sands. Recent C is the C inventory in surface moss/detrital layers above a distinct charred layer (in upland soils) or with $\Delta^{14}C$ values >0‰ (in wetlands). $\Delta^{14}C$ values are inventory-weighted averages for recent C. I, inputs (kg C m^{-2} yr^{-1}); k, decomposition constant ($year^{-1}$); $I - kC_{surf}$, net accumulation rate in surface moss/detrital layers (kg C m^{-2} yr^{-1}); errors are 95% *CI* derived from ^{14}C-age models (Figure 3); all other I and k values were estimated by using the accumulation model described in the text, with recent C and $\Delta^{14}C$ values used as constraints. ND, not determined.

conducted) in 1963 and have since declined as the bomb ^{14}C is diluted through exchange with ocean and terrestrial C reservoirs and by the addition of fossil-fuel-derived CO_2 to the atmosphere.

Bulk ^{14}C values in regrowing moss and detrital layers reflect the recent balance of input and decomposition rates. For example, a site that burned in 1964 with very slow decomposition rates (~0.01 $year^{-1}$ or turnover time of 100 years) would have higher $\Delta^{14}C$ values in the mixed, accumulated moss/detrital layers in 1994 than one with fast decomposition rate (0.1 $year^{-1}$ or ~10 year turnover). The site with slow decomposition would retain nearly all of the C sequestered in the years just after 1964 (when ^{14}C values were at their peak, Figure 1a), while C with elevated ^{14}C values representative of the late 1960s and early 1970s would have been largely lost from the site with fast decomposition rates. In addition, overall C inventory in moss layers would be lower in 1994 for the site with faster decomposition rates, given the same inputs.

We predict the C inventory in moss/detrital layers with known fire history (t = time since fire) for different values of I and k using (1) and (2) above. To determine the inventory-weighted mean $\Delta^{14}C$ value in 1994, we assume annual C additions are labeled with the $\Delta^{14}C$ of that year's atmospheric CO_2 [from *Burcholadze et al.*, 1989] (Figure 1a) and track the loss of C and ^{14}C with time for each year's C input. Isotopes are assumed not to fractionate during decay, i.e., respired C is assumed to have the same ^{14}C content as the organic matter in each annual layer. The equation expressing the inventory-weighted mean ^{14}C content of the soil profile in year t after initiation of accumulation is

$$F_C(t) = \frac{[IF_{atm}(t) + C(t-1)F_C(t-1)(1 - k - \lambda_{14})]}{C(t)} \quad (3)$$

where F_C represents the inventory-weighted ^{14}C content, expressed as the absolute fraction modern, where $F_C = \Delta^{14}C/1000 + 1$; I is the annual C input to moss/detrital layers (in kg C m^{-2} yr^{-1}), $F_{atm}(t)$ is absolute fraction modern ^{14}C in the atmosphere for that year's addition ($F_{atm}(t) = \Delta^{14}C_{atm}(t)/1000 + 1$); k is the decomposition constant ($year^{-1}$); and $\lambda_{^{14}C}$ is the radioactive decay constant for ^{14}C, equal to 1/8267 years. Carbon accumulation of the detrital layer is assumed to start in the year following fire. Values for I and k are adjusted until the model matches both the observed bulk C inventory and the ^{14}C data, listed in Table 1.

^{14}C-age Model: Sites Dominated by Sphagnum

Sphagnum mosses, which grow vertically in a uniform manner, record the atmospheric $^{14}CO_2$ history directly (Figure 1b). We use a plot of cumulative (top-down) C inventory in the profile against age of the carbon (as determined from comparison of $\Delta^{14}C$ in moss with the atmospheric curve) and fit (2) to determine best-fit values for I and k. The age of C is based on picked leaves of sphagnum moss, but C inventory may reflect contributions of vascular plant roots and litter in addition to mosses. We assume that vascular plant inputs decompose at the same rate as moss, that the ^{14}C content of sphagnum mosses reflect the atmospheric ^{14}C for the year in which they grew, and that there is minimal vertical mixing of the accumulating detrital/moss layer.

Deep Organic Layers

Prior to 1950 the ^{14}C content of atmospheric CO_2 was approximately constant. C accumulation for deep organic (below char layers) plus mineral A horizons may be determined using (2). For constant atmospheric ^{14}C content (F_{atm} = 1.0 pre-1960), $F_C(t)$ may be expressed as

$$F_C(t) = \frac{\frac{I}{(k+\lambda_{14})}\left[1-\exp\left(-(k+\lambda_{14})t\right)\right]}{C(t)}, \qquad (4)$$

where t is the time since soil began to form, ~8000 years near Thomspon, Manitoba. Substituting for $C(t)$ [*Trumbore et al.*, 1992],

$$F_C(t) = \frac{k}{(k+\lambda_{14})}\,\frac{\left[1-\exp\left(-(k+\lambda_{14})t\right)\right]}{\left[1-\exp(-kt)\right]} \qquad (5)$$

I and k values may also be fit to a plot of C accumulation versus time derived from the calibrated ^{14}C age [*Stuiver et al.*, 1993], analogous to the ^{14}C-age method described for surface detrital layers.

Results

Soil Carbon Inventory

Figure 2 summarizes carbon content in kg C m^{-2} per cm depth for soils representative of each of the four drainage classes. The two soils from the old black spruce (OBS) site (feather and sphagnum mosses with clay substrate) were frozen at depths of 50–70 cm when they were collected in early August 1994 but were sampled at least to the mineral horizon. Organic peat layers at the tower fen site continue to depths of 3–4 m, though only the uppermost 80 cm are shown in Figure 2.

Table 1 compares C inventories for surface detrital layers with total soil C storage for each soil profile where radiocarbon was measured. Surface detrital layers were defined as all C above charred layers in upland soils and all C with $\Delta^{14}C > 0‰$ in wetlands. Total C inventory includes surface detritus, deep organic and mineral horizons, excluding mineral soil layers that contain significant amounts of $CaCO_3$ that predominantly contain organic C inherited from Lake Agassiz lacustrine clay parent material. Wetland C inventories do not include mineral soil. The inventory-weighted mean $\Delta^{14}C$ values for detrital layers in Table 1 are >100‰, indicating that most of the C in surface mosses was fixed from the atmosphere since the end of thermonuclear weapons testing in 1963. Surface detrital/moss layer C accumulated since the last fire represents 8–38% of the total carbon accumulated in the ~8000 years since the retreat of Lake Agassiz in upland soils. It is apparent from Figure 2 and Table 1 that C average accumulation rates over decadal timescales (~0.3–10 kg C m^{-2} in 30–120 years, or 0.01–0.08 kg C m^{-2} yr^{-1}) are about an order of magnitude greater than those over millennial timescales (~2–30 kg C m^{-2} in 8000 years, or 0.0003–0.004 kg C m^{-2} yr^{-1}). High rates of C accumulation in surface detritus between fires will be offset when this layer burns, so averaged over many fire cycles, slower rates dominate.

Total C inventory and long-term average accumulation rates vary widely with drainage across the NSA BOREAS area (Figure 2, Table 1). Well-drained sites with sandy parent material and jack pine vegetation (NSA OJP and YJP) have the lowest C total inventory, about 1.5–3 kg C m^{-2}. Both jack pine and sand sites show increases in C and ^{14}C in subsurface Bs (sesquioxide B) horizons. The origin of organic matter in these horizons appears to be leaching from the surface horizons, followed by sorption on mineral surfaces at depth [*Moore and Knowles*, 1990]. The carbon in jack pine soil Bs horizons has $\Delta^{14}C$ values of +30 to +72‰, while the average atmospheric $\Delta^{14}C$ between 1960 and 1994 was +370‰. Hence at least ~10% the Bs horizon carbon has been fixed since 1960. One possible reason for low-carbon inventory in well-drained soils is relatively rapid turnover, coupled with a lack of clay mineral surfaces to stabilize C [*Moore and Knowles*, 1990].

Nutrient-rich wetlands (fens) have the largest total C inventory (~100 kg C m^{-2} at the tower flux site) and the most C labeled with bomb ^{14}C (6–11 kg C m^{-2}). The weighted $\Delta^{14}C$ values calculated for surface layers are +200 to +300‰. Constant accumulation of carbon with no decomposition would yield $\Delta^{14}C$ values of the atmospheric average since 1960, ~+370‰. Hence $\Delta^{14}C$ values between +200 and +300‰ observed in surface portions of wetland soils indicate decomposition rates are slow enough that much of the C fixed during the past decades remains undecomposed.

Upland sites on clay soils with moderate-to-poor drainage have intermediate C inventory in postfire layers. Carbon storage in surface detritus increases with time since fire (Table 1) [*Harden et al.*, this issue]. Deep organic layers (humic or O horizons) with very high carbon densities are responsible for most of the difference in total C inventory observed between better drained sites (where organic layers are thin) and poorly drained sites (where they are thicker; see Figure 1). $\Delta^{14}C$ values in surface mosses at the OBS site are higher for poorly drained sites with sphagnum (+160 to +260‰) than moderately drained sites with feathermoss (+110 to +190‰). Surface detritus at both sites began accumulating C after a fire ~117 years ago (S. T. Gower, personal communication, 1996), and thus were subject to inputs of moss and detritus fixed between ~1900 and 1960 A.D. which should dilute the bomb ^{14}C signal. Lower ^{14}C values may be indicative of overall slower C turnover rates for moderately drained feathermoss/black spruce stands, since lower ^{14}C values indicate dilution of bomb C with a greater proportion of prebomb organic matter.

Charcoal isolated from a deep organic layer in a poorly drained soil profile (Figure 2c) made up ~50% of the total carbon in the layer, suggesting that incomplete burning as well as slower decomposition may contribute to higher deep organic C stores in wetter soils. $\Delta^{14}C$ values for charcoal and the bulk organics from which it was extracted were similar.

Carbon Input and Decomposition Rates in Surface Detrital and Moss Layers

Values of I and k that reproduce the observed surface moss/detritus C and ^{14}C inventory are reported together with observations in Table 1. These values are compared with I and k values derived by using the ^{14}C-age model for upland sphag-

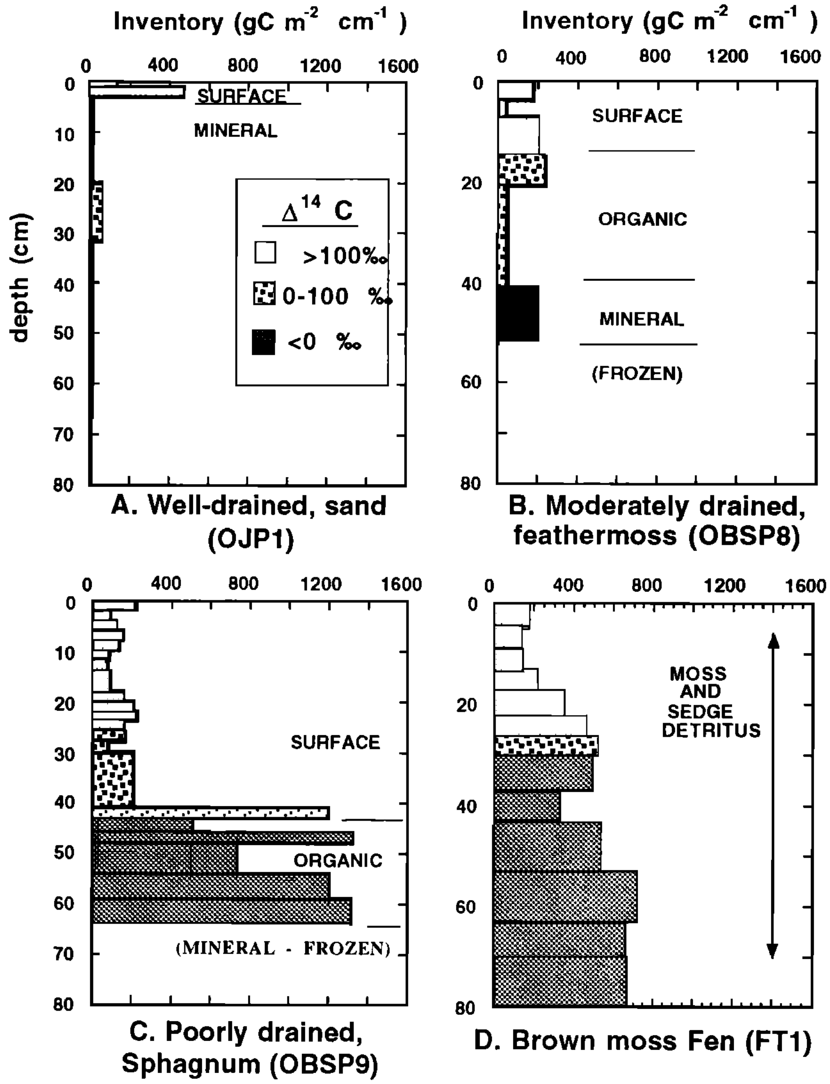

Figure 2. Carbon inventory with depth for the four major drainage classes. Detrital, organic, and mineral horizons are identified. Sites depicted are OJP (old jack pine), OBSP8 (old black spruce with feathermoss), OBSP9 (old black spruce with Sphagnum), and the NSA tower fen (brown moss and sedge). Zero depth in each case is defined as the surface of the living moss or lichen. The thickness of each bar represents the depth integrated during sampling. The shading identifies layers obviously dominated by C fixed over the past 30 years (postbomb C, >100‰ in $\Delta^{14}C$), layers that are dominated by C fixed more than a century ago (<0‰ in $\Delta^{14}C$), and layers that either contain a mixture of the first two components or represent C fixed between about 1955 and 1962 (0–100‰ in $\Delta^{14}C$). Layers with $\Delta^{14}C$ values >100‰ are typically living and dead mosses at the top of the soil profile.

num and wetland sites (Figure 3 and values identified in Table 1). For the six sites with sphagnum where both models were used, I and k values derived by using the two models were in accord.

For upland sites where C inputs from vascular plants are important and where upward moss growth is not so regular as in sphagnum-dominated sites, further discussion of the meaning of I and k values derived by using moss accumulation models is required. First, the I and k values derived from radiocarbon-based models are average values that can describe the dynamics of the surface detrital layer as a whole. For sites with dense tree cover which are well to moderately drained, C inputs range from moss growth to conifer needles to roots and woody debris. Moss and conifer needles decompose more rapidly than roots and woody debris [*Hobbie*, 1996]. While jack pine roots in sandy soils extend deep into the mineral soil and are not important in surface detrital layers, roots of black spruce on clay soils accumulate in a mat at the base of the surface moss/detrital layer. Hence slow decomposition of roots may cause average turnover times derived for moderately drained sites with feathermoss (0.003 to 0.025 1/year, or turnover times of 40–330 years) to be longer than those for sphagnum-dominated sites nearby which have little or no tree cover (0.016–0.027 1/year or turnover times of 37–62 years) or sand/jack pine sites (0.07–0.17 1/year, 6–15 years).

Our radiocarbon modeling approach assumes C inputs in any given year have $\Delta^{14}C$ values equal to the atmosphere for that year. While this is likely true for moss, deciduous leaf, and fine root inputs to soil, other litter inputs in boreal sites with dense tree canopies may not meet this assumption. Conifer

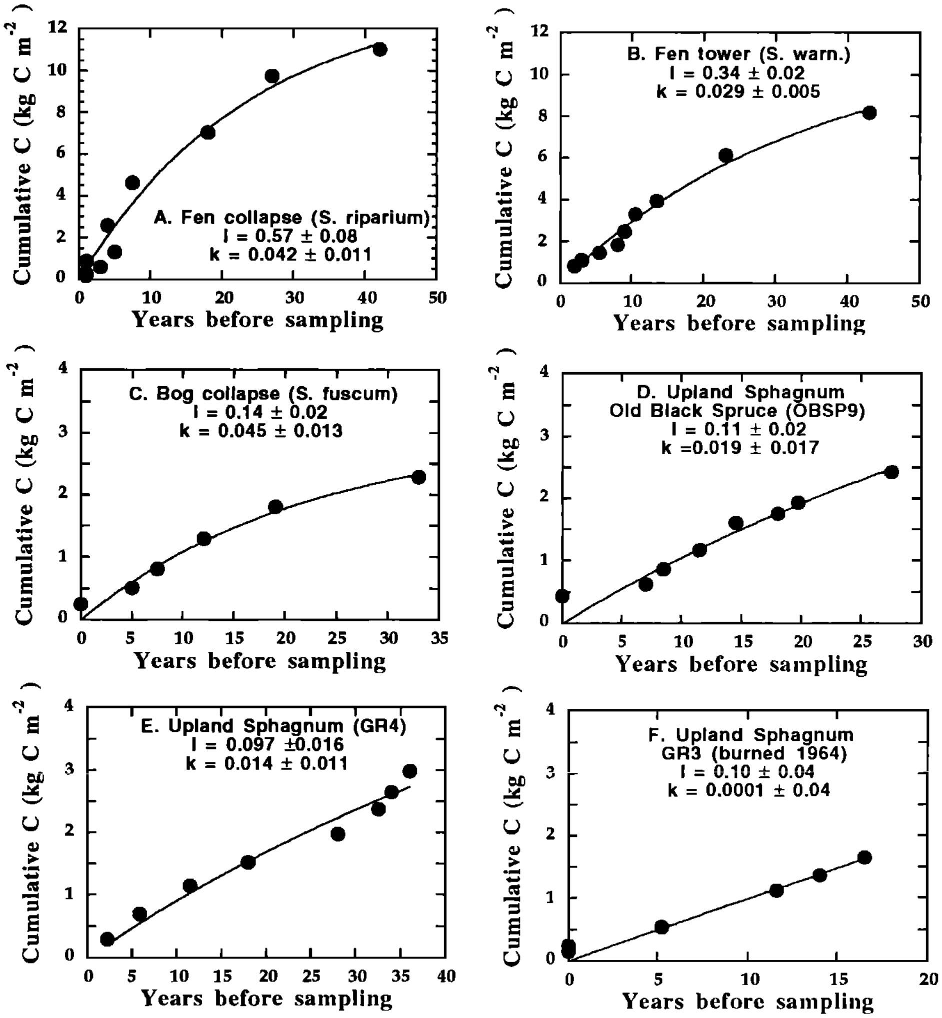

Figure 3. Plots of cumulative C inventory (with zero at the top of the living moss layer) versus the age of the C in a given layer for sites with sphagnum moss cover. Ages are derived from comparing $\Delta^{14}C$ values for picked and cleaned sphagnum leaves with the atmospheric curve (Figure 1a). Input (*I*) and decomposition rates (*k*) derived from fitting equation (2) in the text are shown with the curve fit. The errors are 95% confidence intervals for *I* and *k* values.

needles reside on trees for several years before falling and therefore would be expected to have $\Delta^{14}C$ values greater than the atmosphere in the year they are added to surface detrital/moss layers. Turnover times derived for sites where conifer needles dominate will reflect both the time that needles reside on trees and the time required for decomposition. Alternatively, woody debris, especially the charred remnants of trees burned in the last fire, are decades to a century old when they the enter the detrital layer and will dilute the ^{14}C content of other litter components and result in longer turnover times. Dilution of ^{14}C with organic matter derived from woody debris may account for slower turnover times derived in moderately drained feather moss/black spruce sites; charred and woody material were more easily seen and we avoided sampling them in sand/jack pine sites, where moss cover is thinner.

To determine the effects of inhomogeneity in litter cohort ^{14}C values, we separated and measured litter components at two sites. The surface detrital layer at one moderately drained site burned in 1964 with clay soil (GR1, Table 2) had bulk $\Delta^{14}C$ values of +190‰, while litter components ranged from −39‰ (charcoal) to +244‰ (jack pine and black spruce needles). For comparison the $\Delta^{14}C$ of atmospheric CO_2 in 1994 was ~+120‰. Figure 4 shows the ^{14}C content of different litter cohorts with depth for a feather moss layer at the old black spruce site and compares these to the C inventory and $\Delta^{14}C$ predicted by the accumulation model for bulk organic carbon. Needles at all depths have higher $\Delta^{14}C$ values than coexisting mosses. The magnitude of the difference indicates that the black spruce needles on average are ~10 years old before falling and getting incorporated into the detrital layer. The abundances of different cohorts changes with depth. Moss accounts for ~60% of the carbon in the 0–4 cm layer but decreases in abundance with depth. Needles and twigs make up ~30% of the carbon in the uppermost horizon; needle abundance also decreases with depth. Most of the carbon at depths >20 cm is associated with fine roots or material that has broken into small enough pieces that it is difficult to identify and quantify. The low $\Delta^{14}C$ values of roots, which make up the majority of C deep in the soil profile, reflect slow rates of decomposition of woody material.

Finally, as noted in Table 2, we were unable to reproduce both C inventory and $\Delta^{14}C$ values for the more recently burned

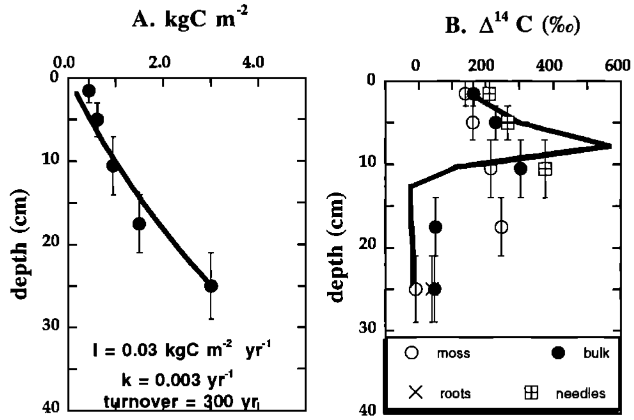

Figure 4. C inventory (cumulative, with 0 at the moss surface) and $\Delta^{14}C$ values for bulk organic matter and litter cohorts with depth for a feather moss/detrital layers at the OBS site. Solid lines are values predicted by the vertical accumulation model (equations (2) and (3), converted to depth using observed bulk density data). $\Delta^{14}C$ data were obtained for bulk samples (ground to <100 mesh: solid circles), moss (open circles), black spruce needles (squares), and fine roots (crosses, measured for 20–30 cm interval only). Moss and needles are the most important components in the upper 10 cm, while roots and material too fine to pick for identifiable macrofossils were most abundant in the 20–30 cm layer.

sites (1964 and 1956 burns) on moderately drained feather moss/black spruce sites using the moss accumulation model. In each case, the $\Delta^{14}C$ values calculated by the model exceeded observed values in the detrital layers. One explanation is the inclusion of charred woody debris in the moss/detrital layer. In Table 1 the lowest $\Delta^{14}C$ value for the bulk detrital layer (for site SOAB 8, which burned in 1956) is +85‰. The field notes for that site note the presence of a decomposed log in the sampled detrital layer. Trees burned in the 1956 fire contained little or no bomb radiocarbon, thus the decomposing wood (now overgrown with moss) dilutes the ^{14}C content of this detrital layer compared to other samples. Additionally, the assumption that C inputs to soil are constant with time and begin the year after fire may be an oversimplification, especially for well- and moderately drained sites. Field observations [*Harden et al.*, this issue] show <3% areal coverage by feather mosses in some recently burned areas, with moss and detrital layers remaining patchy even 30 years following fire. Thus the time lag between the fire and the initiation of significant litter inputs can be several years to a decade or more. Observations of C and ^{14}C inventory in moderately drained 30–38 year old burn sites (Table 1) are reproduced by the model only by assuming at least a 15 year lag between the fire and the first C inputs. The model works well for sites that burned >100 years ago because there were no dramatic changes in atmospheric ^{14}C in the first decades following fire and because the time since fire is long compared to a potential time lag.

In summary, k values derived from modeling of radiocarbon in soil detrital layers will reflect the average residence time of C in the ecosystem. In sites where woody debris may be an important component of litterfall, turnover times derived from ^{14}C may be longer than timescales for decomposition alone because the litter material is already "old" when it enters the soil. The sites most affected by this potential bias in the boreal NSA are moderately drained sites with feathermoss and dense black spruce stands. Sites on well-drained sand with jack pine trees, which potentially have the same effects from woody debris inputs, are not affected in this study because obvious woody debris could be seen and was avoided during sampling.

C Balance in Deep Organic Layers

Figure 5 shows C accumulation versus time curves derived from vertical profiles of C combined with ^{14}C measurements of prebomb organic matter for four sites, representing fens, poorly drained sites with sphagnum, and moderately drained sites with feathermoss on clay substrate. I and k values from the ^{14}C-age model (Figure 5) are compared with those derived by using the accumulation model (equation (2) and (4)) based on the inventory-weighted mean ^{14}C content for C accumulated over the past 8000 years (assuming no bomb ^{14}C inputs).

For well-drained sand/jack pine sites, deeper soil layers had bomb ^{14}C, indicating relatively rapid turnover compared to the

Table 2. Long-Term Input and Decomposition for Deep Organic Layers

						$I - kC_{deep}$	
	kg C m^{-2}	$I(1)$	$k(1)$	$I(2)$	$k(2)$	(1)	(2)
	Well-Drained Sand/Jack Pine						
Old jack pine	1.5	···	···	0.015	0.01	···	0
	Moderately Drained Feather Moss						
Old black spruce (OBSP11)	7	0.005	0.0006	(0.002)	(0.006)	0.001	(−0.04)
	Poorly Drained Sphagnum						
S. warnstorfii (GR4)	12	(0.009)	0.0008	0.031	0.002	(−0.001)	0.007
S. warnstorfii (OBSP9)	20	0.028	0.0009	0.033	0.0007	0.010	0.019
S. fuscum (GR3) burned 1964	11	0.007	0.0005	0.014	0.0008	0.002	0.005
	Wetland						
Tower fen	100	0.038	0.0004	0.064	0.0005	0.008	0.0014
Palsa (frozen fen)	100	0.020	0.0002	0.039	0.0002	0	0.019

Deep C inventory (kg C m^{-2}) is the difference of total and recent C inventory values given in Table 1. $I(1)$ and $I(2)$ are inputs to the deep organic layer (kg C m^{-2} yr^{-1}) derived by using the total C and ^{14}C accumulated over the past 8000 years (1) and from ^{14}C-age models in Figure 5 (2); $k(1)$ and $k(2)$ are the decomposition constants (year^{-1}) derived by using the same two approaches. Net deep organic layer C flux is $I - kC_{deep}$ (kg C m^{-2} yr^{-1}) for both models (1) and (2). Values in parentheses indicate that negative net fluxes resulted: these scenarios were not deemed reasonable and were not used in further calculations.

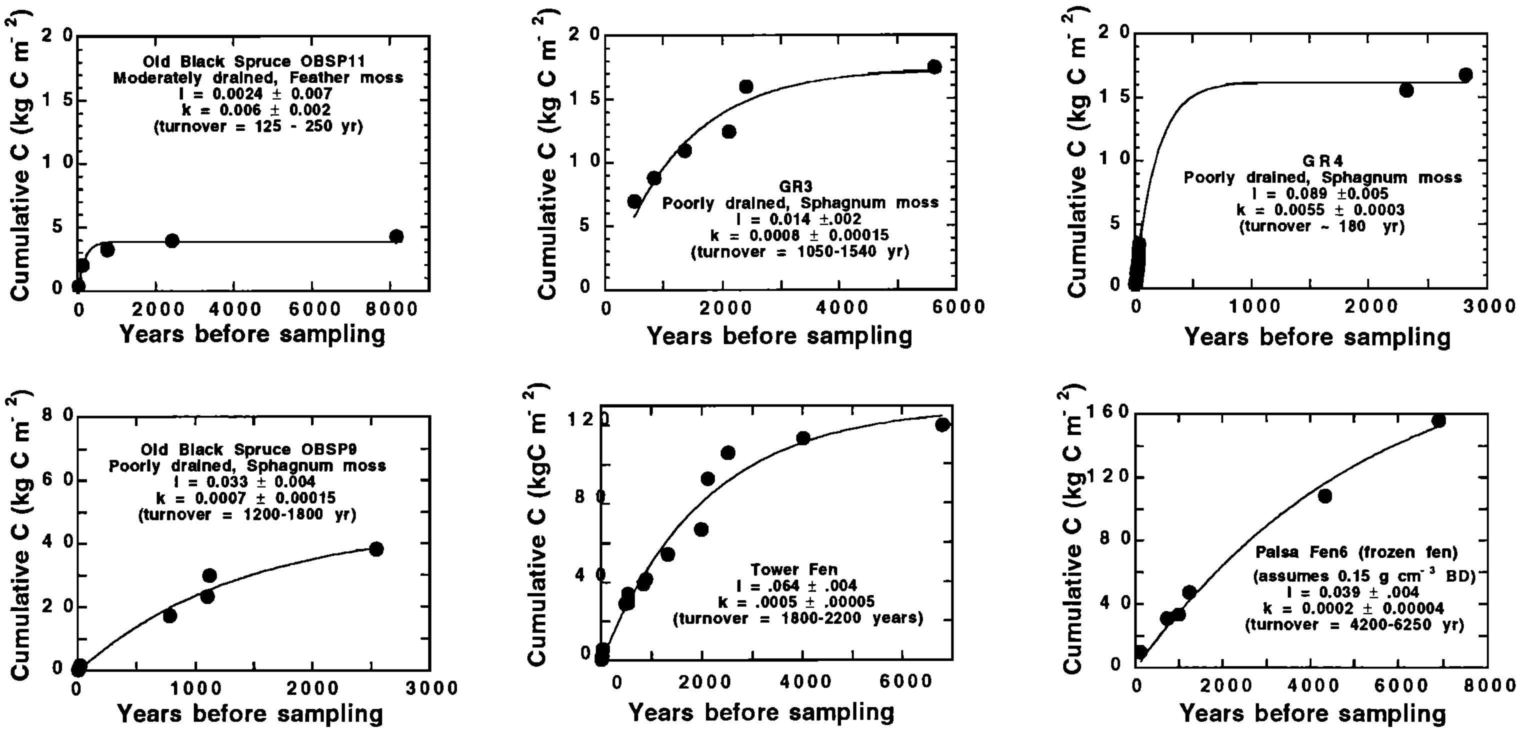

Figure 5. Derivation of long-term accumulation rates from equation (2) fit to a plot of net C accumulation as a function of time. Time is derived from ^{14}C ages (converted to calendar ages) of hand-picked sedge or moss macrofossils (in the fen) and bulk organic matter (carbonate free) for humus and mineral soil layers. Errors are 95% confidence intervals for the curve-fit parameters. All sites are upland clay soils or wetlands; the approach for estimating I and k for jack pine/sand soils is described in the text.

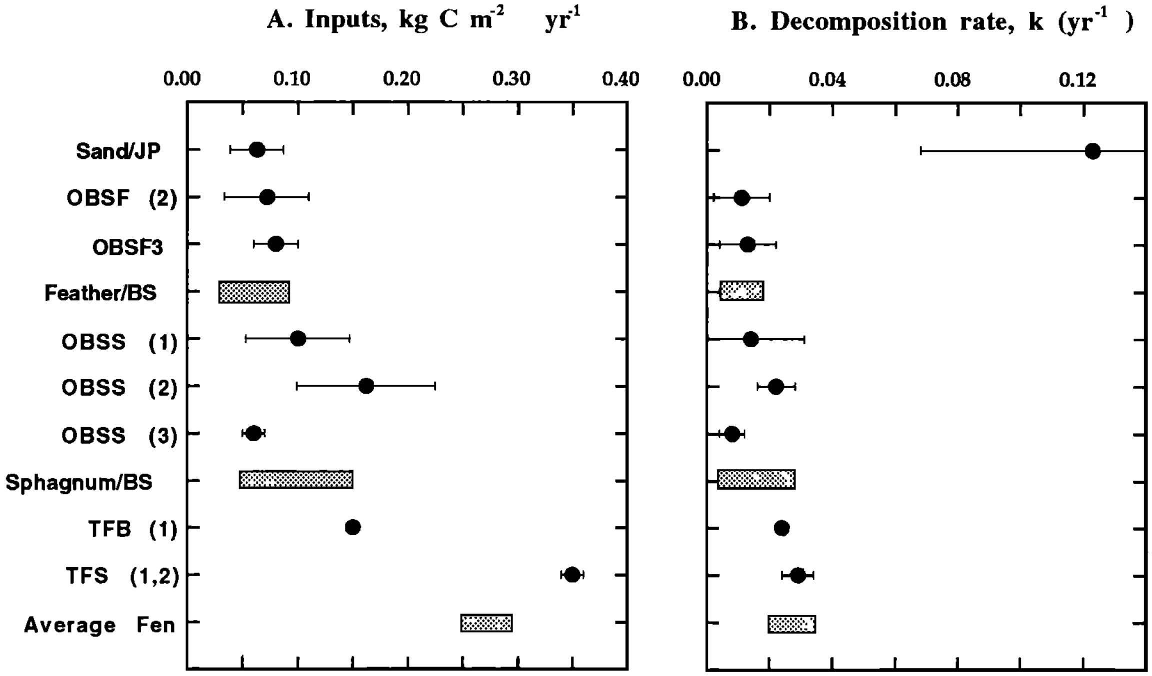

Figure 6. Comparison of average input and decomposition (I and k) values derived for surface/moss layers using accumulation model 1, ^{14}C-age model 2, and chronosequence model 3 for soils representing the four major drainage classes identified in this study. Shaded regions show the values used as best estimates for I and k based on overlap among the different models (C values given in Table 3).

~8000 years of soil development. In this case, we determined I and k values by assuming that the carbon stored in mineral soil horizons is at steady state [*Trumbore et al.*, 1996]. The $\Delta^{14}C$ values of organic matter in mineral soil horizons in YJP and OJP soils sampled in 1994 are between +30 and +80‰. For a soil at steady state, these are consistent with decay constants of 0.007–0.012 year^{-1} (turnover times of 80–140 years [*Trumbore et al.*, 1996]). Input values are then calculated as kC, where C is the C inventory in deep organic carbon.

Input rates of C to deep organic layers range from 0.005 to 0.06 kg C m^{-2} yr^{-1}, with highest values in fens. Inputs in upland soils are charred material after fire and/or leached organics that are translocated downward through the soil profile, while in wetlands, inputs are those components of recent C which are pushed below the water table. Decomposition constants appear to be related to soil parent material and drainage, with turnover times for deep organic matter of ~100 years in well-drained sand soils and 1000–5000 years in clay soils and wetlands. Accumulation rates of deep soil C, calculated as $I - kC$ in Table 2, are similar to those derived by dividing C inventory by the 8000 years of soil development.

A check on decomposition rates in Table 2 for upland soils may be obtained from observed winter CO_2 fluxes. Temperatures in surface detrital layers drop below −6°C by early February at OBS sites, while temperatures in organic layers below remain high enough for decomposition to take place [*Winston et al.*, this issue]. Radiocarbon measurements of CO_2 confirm that decomposition of older organic matter is a major component of the winter CO_2 flux [*Winston et al.*, this issue]. Assuming decomposition of organic and mineral layer carbon in the source of winter soil respiration, this flux should equal the product of deep soil decomposition rate and C inventory. Observations of winter CO_2 flux are available everywhere but the NSA fen tower site [*Winston et al.*, this issue]. Fluxes differ little between sites in midwinter. We assume a value of ~4 mg C m^{-2} hr^{-1}, which, assuming deep soil temperatures increase above −5°C for ~3 months of the year [*Winston et al.*, this issue], yields a net CO_2 flux from the deep soil of 0.009 kg C m^{-2} yr^{-1}. Dividing this by the average deep organic C inventory (18 kg C m^{-2} for sphagnum, 8 kg C m^{-2} for feather moss sites, and 1.5 kg C m^{-2} for sand/jack pine sites) yields decomposition rates of 0.0005, 0.001, and 0.008 year^{-1}, or turnover times of 2000, 1000, and 125 years, respectively, in accord with values in Table 2. This calculation assumes that sources of CO_2 deeper in the soil are unimportant during winter.

Discussion

Drainage Control of *I* and *k* in Surface Layers

Figure 6 compares the average I and k values derived by using accumulation, ^{14}C age, and fire chronosequence [*Harden et al.*, this issue] modeling approaches. On the basis of the overlap among I and k values among the three estimates, we identify the range of most likely values for I and k in surface detrital/moss layers. Table 3 summarizes the range of I and k values for the soils at the four NSA tower sites (YJP, OJP, OBS, and the tower fen). Because of differences in C accumulation rates derived for brown mosses versus sphagnum-dominated regimes present at the tower fen, we assumed on average the fen had 33% brown moss and 67% sphagnum cover.

Annual average inputs (I) to surface detrital/moss layers (Table 1 and 3) are greatest at nutrient-rich wetland (fen) sites (0.2 to nearly 0.6 kg C m^{-2} yr^{-1}) compared to nutrient-poor bogs and upland sites (0.02–0.15 kg C m^{-2} yr^{-1}). These estimates indicate annual below-ground and aboveground C inputs averaged over the past several decades. For comparison, moss net primary production ranged from ~0.15 kg C m^{-2}

Table 3. Best Estimates for Annual C Balance in Four Drainage Classes

I_{surf}	±	k_{surf}	±	TT_{surf}	$I - kC_{surf}$	±	TT_{deep}	kC_{deep}	Net	±	%TR
					Jack Pine, Well Drained						
0.06	0.02	0.123	0.055	6–15	0.007	0.005	100	0.012	−0.005	0.007	22
					Old Black Spruce, Feather						
0.06	0.03	0.011	0.007	56–250	0.016	0.013	1600	0.004	0.012	0.013	9
					Old Black Spruce Sphagnum						
0.10	0.05	0.016	0.012	36–250	0.015	0.013	1430	0.012	0.003	0.058	14
					Tower Fen, 33% Scorpidium and 67% Sphagnum						
0.28	0.08	0.027	0.005	31–45	0.019	0.006	3300	0.030	0.027	0.013	11

Best estimates of I_{surf}, k_{surf}, TT_{surf} (annual inputs in kg C m^{-2} yr^{-1}, decomposition constant in $year^{-1}$, and turnover time ($1/k$, in years) for surface detritus/moss layer) based on overlap of values from the three models (shaded regions in Figure 6). TT_{deep} is the turnover time in years for deep organic layers ($= 1/k_{deep}$), kC_{deep} is the annual decomposition flux of C from deep organic layers (in kg C m^{-2} yr^{-1}). Net accumulation for the whole soil profile is $I - kC_{surf} - kC_{deep}$ and is given in kg C m^{-2} yr^{-1}. Errors are estimated from standard deviation of all data in Table 1 (accumulation model), or 95% confidence intervals (^{14}C age and chronosequence data). Errors for net fluxes are obtained by propagating errors in I and k. %TR is the percent of total soil decomposition flux due to decay of deep organic carbon in humic and mineral layers.

yr^{-1} for *S. riparium* in a highly productive fen to 0.05–0.10 kg C m^{-2} yr^{-1} for brown mosses and *S. warnstorfii* at the tower fen site and 0.01–0.04 kg C m^{-2} yr^{-1} for sphagnum and feathermoss at the old black spruce site (J. Bubier, University of New Hampshire, personal communication, 1996). Higher inputs derived from the ^{14}C approach may be explained if C inputs from sedges and shrubs in wetlands and shrub litter and roots in upland sites are significant. Estimates of litterfall and fine root production by trees in upland sites are similar to those for moss production (S. T. Gower, personal communication). Productivity estimates for sedges and shrubs in wetlands were not available but by our estimates would account for more than half of annual net production in wetland sites.

In general, decomposition rates in surface detrital layers are slowest for upland sites on clay (turnover times of 30–500 years) and fastest at the jack pine sites (5–15 years). As discussed previously, estimates of turnover at sites with large potential inputs from woody debris and charcoal (feathermoss-dominated sites) may be overestimates of decomposition rates. The difference between wetland and upland moss layer decomposition rates may derive from the lack of woody inputs in bogs and fens. Nonetheless, even the lowest values (~30 years) we obtain for moss-dominated detrital layers on clay soils are longer than those reported in the literature (~5 years) [*Oechel and Van Cleve*, 1986] and used in models [*Bonan*, 1990]. The short turnover times derived from the data reported by *Oechel and Van Cleve* [1986] are based on the ratio of moss NPP to total moss layer inventory. If the moss layer is accumulating, the assumption of steady state will lead to an underestimate of turnover time. Our results are more consistent with long residence times reported for black spruce forest floor in Alaska (36–111 years) [*Van Cleve and Yarie*, 1986], and decomposition rates reported for Sphagnum [*Kuhry and Vitt*, 1996; *Rochefort et al.*, 1990], and conifer needles [*Flanagan and Van Cleve*, 1983; *Fox and Van Cleve*, 1983].

Several factors have been identified as controlling rates of decomposition on annual to decadal timescales in boreal forest soils, including temperature, substrate quality, and soil drainage [*Clymo*, 1984; *Flanagan and Van Cleve*, 1983; *Van Cleve et al.*, 1991; *Van Cleve and Yarie*, 1986]. On long timescales, drainage dominates turnover, resulting in the buildup of large inventories of soil C since the drying of Lake Agassiz ~8000 years ago, in the decrease in C turnover rates with depth in poorly drained soils and wetlands, and from well-drained to poorly drained soils (Table 2). Drainage apparently has less effect on decomposition rates in detrital layers (including the aerobic portions of wetlands). Soil temperatures in July are highest in the fen tower (~16°C at 10 cm [*Bubier et al.*, 1995] and TF data) and sand sites (YJP, ~13°C; OJP ~10°C, both measured at 10 cm), where fastest decomposition rates are observed (Table 1). Clay soils with permafrost under mature black spruce canopies have the coldest soil temperature in July (6°–11°C at 10 cm; data from P. Crill, TGB1).

Net C Accumulation Rates

All sites on clay substrate are accumulating C in surface detrital/moss layers in 1994, with fastest rates in the fen (Table 1, $I_{surface} - k_{surface}C_{surface}$). Accumulation rates calculated for surface layers are 20–45% of estimated annual C inputs to detrital layers in 1994. It is important to note that these rates do not account for horizontal regrowth of moss following fire, which for upland soils may also be an important factor in determining the rate of C sequestration [see *Harden et al.*, this issue]. These short-term "apparent" C accumulation rates (apparent because they do not represent net C storage for the whole profile because they are offset by net decomposition of C in deeper soil layers) in Table 2 are in the range of values reported in the literature for wetlands (0.04–0.112 kg C m^{-2} yr^{-1} [*Tolonen et al.*, 1992] and for *S. fuscum* (0.013 to 0.035 kg C m^{-2} yr^{-1} [*Kuhry and Vitt*, 1996]).

Apparent deep-soil accumulation rates (inputs to deep organic layers minus deep decomposition, Table 2) are an order of magnitude smaller than short-term apparent accumulation rates calculated for mosses (Table 2, Figure 7a). Comparison of short-term accumulation rates of carbon in surface detritus/moss layers with long-term inputs to deeper soil layers (Tables 2 and 3) shows that carbon accumulation in mosses at the surface are more than sufficient to supply carbon to deep soil layers. One critical connection between short- and long-term accumulation in upland soils is through fire. Charcoal is ubiquitous in boreal forest soils, and each time moss layers burn, more is added to deeper soil layers. Presumably, the more decomposable elements of organic matter associated with fire are leached DOC which may accumulate through sorption on mineral or charcoal surfaces. Increases in organic carbon in mineral soil layers are observed just after fire [*Dyrness and Norum*, 1983] as well as at the leading edge of paludification [*Turunen and Tolonen*, 1996]. Another potential source of de-

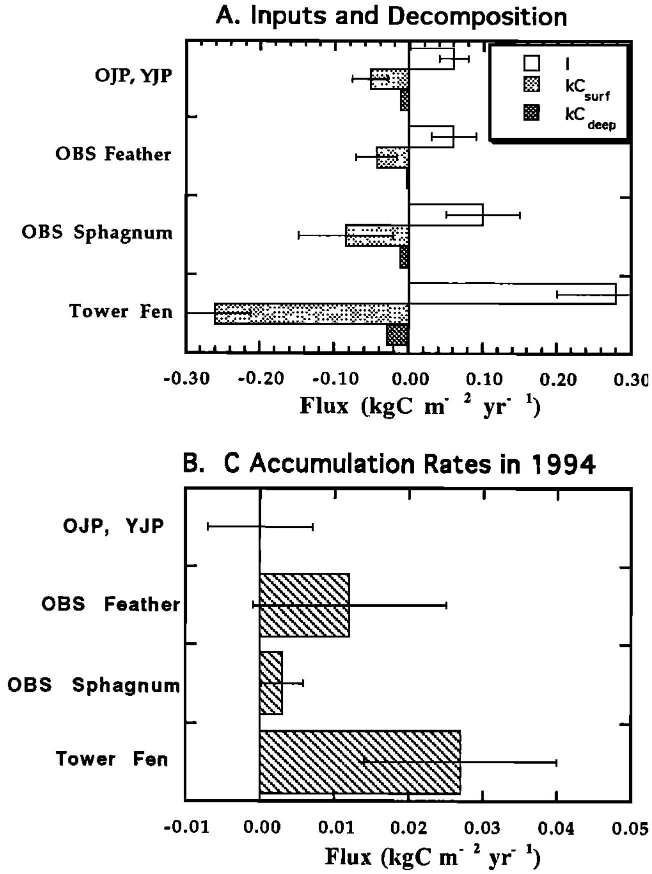

Figure 7. Histograms summarizing the C balance in surface moss layers, deep soil layers, and the total soil. All fluxes are in kg C m^{-2} yr^{-1}. (a) Inputs (I, positive values) and losses by decomposition in surface detrital layers ($kC1$, negative values) and organic/mineral soil layers ($kC2$, negative values). Average rates taken from Tables 2 and 3. Feather and sphagnum moss sites represent mature forest stands, like the NSA OBS sites. Because large variation was seen in among the fen vegetation types (Figure 6), we assumed the tower fen area had roughly two-thirds sphagnum and one-third brown moss. (b) Total net accumulation of carbon, calculated as moss surface inputs minus decomposition fluxes in moss and deep soil layers. Error bars are derived from averaging model-derived I and k values in Tables 2 and 3 (for OBS soils), or from propagating 95% confidence intervals from curve fitting.

composable C to deeper soil layers is leaching of organic matter from dead vascular plant detritus, including woody biomass from fallen trees killed by a previous fire.

Total carbon accumulation rates (Table 3, Figure 7b) calculated for the four main drainage classes equal the annual C inputs to surface detrital/moss layers minus decomposition fluxes from surface and deep organic layers. This calculation assumes that inputs to the deep soil are ultimately derived from moss layers; therefore we do not add inputs to deep organic layers (Table 2) to inputs to surface layers (Table 1) but use values in Table 1 only. For wetland soils the model of *Clymo* [1984] links short- and long-term accumulation rates when decomposed organic matter passes from aerobic to anaerobic (waterlogged) conditions. In this scenario, high rates of C input in surface layers are largely balanced by aerobic decomposition losses, with remaining carbon decomposing more slowly when it is pushed below the water table. Total C accumulation rates predicted here for the tower fen (0.027 kg C m^{-2} yr^{-1}) are in the range of literature values (~0.017 kg C m^{-2} yr^{-1} for fens in Finland [*Tolonen and Turunen*, 1996], 0.027 kg C m^{-2} yr^{-1} for sedge fens in Maine [*Tolonen et al.*, 1992]).

An important assumption made in calculating total C fluxes for Table 2 and Figure 7b is that C addition to deeper soil layers occurs episodically, through fire, in upland soils. Thus for the decadal C balance in these soils, we calculate the net flux as in the wetlands (as surface inputs minus kC for surface detritus minus kC for organic and mineral layers). In uplands this assumes net loss of C in organic and mineral layers between episodes of C addition (fires). We assume inputs and losses to B horizon layers in well-drained sands to be in steady state. Values for upland soils range from 0.000 ± 0.007 kg C m^{-2} yr^{-1} in sand/jack pine soils to 0.003–0.012 kg C m^{-2} yr^{-1} for OBS sites on clay, with most of the net accumulation occurring in moss/detrital layers. On millennial timescales, averaging over many fire cycles, surface accumulation will be balanced by fire, and the net flux will equal the deep inputs minus decomposition in the deep soil, <0.01 kg C m^{-2} yr^{-1} in all upland soils (Table 2). These values range from 0.001 to 0.02 kg C m^{-2} yr^{-1}, with highest values in wetlands.

The fraction of total heterotrophic respiration derived from decomposition in deep organic and mineral soil layers is estimated as $k_{\text{surface}}C_{\text{surface}}/k_{\text{deep}}C_{\text{deep}}$ in Table 3. Estimates range from 9 to 22% of the total soil decomposition flux.

Implications for the Capacity of Soils to Act As Sources or Sinks

The values for net accumulation and respiration derived from soil C and ^{14}C inventories are long-term (decadal or millennial) averages. The C balance in any given year may deviate from this long-term picture. An early spring or exceptionally good growing season conditions can cause a large increase in net sequestration of C in moss and trees, while decomposition rates may remain largely unchanged. Alternatively, warmer soils in winter lead to increased loss of C presumably through increased decomposition in deeper soil layers [*Winston et al.*, this issue]. Thus offsets between input and decomposition may be large in any given year, though mostly in balance when averaged over several decades. Given constant respiration rates, a temporary increase of 0.01 kg C m^{-2} yr^{-1} in the decadal-average net C storage rate would require a 10–17% increase in surface C inputs (primary production) of upland soils and only a 3% increase for fen sites. Increases in NPP would be offset by increased decomposition only after several decades due to slow decomposition rates in these systems.

The total C accumulation rates observed in mature forest ecosystems of the BOREAS NSA should not be used to estimate regional C storage rates directly. The model of C accumulation derived in this paper predicts that the overall C balance will evolve over the cycle of fire in upland systems. For example, if I and k values in regrowing detrital/moss layers remains constant, C accumulation rates should slow with time since fire as slow decomposition of the thickening detrital layer increasingly offsets C addition to surface layers. In addition, the rates derived here apply only to vertical accumulation rates of C in soils and ignore effects associated with horizontal spread of regrowing mosses following fire. *Harden et al.* [this issue] discuss this issue in greater detail and make a spatial extrapolation of annual C balance for the OBS tower footprint.

Regional extrapolations of soil C inventory and fluxes must account for the balance of burned areas with relatively rapid C accumulation in upland moss following fire and for the evolution of wetlands.

Conclusions

We used vertical profiles of carbon and radiocarbon to determine rates of carbon input, accumulation, and turnover in the four main soil types present in the BOREAS northern study area (sand with jack pine, well-drained clay with feather moss, poorly drained clay with sphagnum, and wetlands). Inputs and decay rates are quite different between sites, with highest annual rates of C addition in fens and fastest turnover rates in sands. Rates of input, accumulation, and turnover in postfire surface detrital layers (living and dead mosses and surface detritus) are roughly an order of magnitude larger and faster than in organic and in mineral soil horizons.

All systems except the sand/jack pine sites are accumulating carbon in soils in 1994. Total C accumulation rates represent the difference of much larger fluxes representing annual C addition to and loss from soils (Figure 7a, Table 3). Most of the C accumulating in 1994 is added to surface organic layers, where decomposition rates are slow compared to removal by fire in upland systems. Carbon fluxes derived from input and decomposition rates based on C and ^{14}C data represent average rates of C accumulation and loss over the last several decades. Because of the long average time interval between C addition to soil and subsequent loss by decomposition, observations in a given year may deviate from the long-term average. Inputs derived from modeling C and ^{14}C inventory in surface moss/detrital layers compare favorably with other estimates of annual C additions to soil.

Site history, including the time since fire and the long-term history of C accumulation, matters in that it determines present-day heterotrophic respiration and therefore the status of the soil as a sink of C. Over millennial timescales that average over many fire cycles, C accumulation rates are an order of magnitude smaller than those derived for recent decades.

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