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Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape

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Abstract. Boreal forests and wetlands are thought to be significant carbon sinks, and they could become net C sources as the Earth warms. Most of the C of boreal forest ecosystems is stored in the moss layer and in the soil. The objective of this study was to estimate soil C stocks (including moss layers) and rates of accumulation and loss for a 733 km^2 area of the BOReal Ecosystem-Atmosphere Study site in northern Manitoba, using data from smaller-scale intensive field studies. A simple process-based model developed from measurements of soil C inventories and radiocarbon was used to relate soil C storage and dynamics to soil drainage and forest stand age. Soil C stocks covary with soil drainage class, with the largest C stocks occurring in poorly drained sites. Estimated rates of soil C accumulation or loss are sensitive to the estimated decomposition constants for the large pool of deep soil C, and improved understanding of deep soil C decomposition is needed. While the upper moss layers regrow and accumulate C after fires, the deep C dynamics vary across the landscape, from a small net sink to a significant source. Estimated net soil C accumulation, averaged for the entire 733 km^2 area, was 20 g C m^{-2} yr^{-1} (28 g C m^{-2} yr^{-1} accumulation in surface mosses offset by 8 g C m^{-2} yr^{-1} lost from deep C pools) in a year with no fire. Most of the C accumulated in poorly and very poorly drained soils (peatlands and wetlands). Burning of the moss layer in only 1% of uplands would offset the C stored in the remaining 99% of the area. Significant interannual variability in C storage is expected because of the irregular occurrence of fire in space and time. The effects of climate change and management on fire frequency and on decomposition of immense deep soil C stocks are key to understanding future C budgets in boreal forests.

1. Introduction

Boreal forests play an important role in the global carbon budget. Of the 1500 petagrams (1 Pg = 10^{15} g) of C stored in soils globally and 600 Pg of C in aboveground biomass [*Reeburgh*, 1997], about one third of this global terrestrial C is found in the biomass, detritus, soil, and peat pools of the boreal forest biome, with about three fourths of the C in boreal forest biome stored belowground [*Apps et al.*, 1993; *Peng et al.*, 1998]. Predicting how these vast stores of soil C in the boreal forest biome will be affected by future climate change requires an understanding of the factors controlling the production, decomposition, and storage of organic C in boreal ecosystems.

Inverse models that calculate the latitudinal distribution of CO_2 sources and sinks from observed CO_2 and $^{13}CO_2$ distributions suggest that boreal regions may be significant C sinks [*Tans et al.*, 1990; *Ciais et al.*, 1995]. An alternative approach to determining C exchange at the landscape or regional scale is to develop process models of C dynamics and to use those models, together with a knowledge of the spatial distribution of important forcing factors, to extrapolate field measurements of C losses and gains to regional scales. Because it is process-based, the latter approach may also be used to predict the response of the landscape to changes in forcing parameters. Responses of boreal forest soils to warming, changes in drainage, or changes in fire frequency have all been proposed to be important for terrestrial C storage [*Bonan*, 1993; *Moore and Knowles*, 1990; *Gorham*, 1991; *Kasischke et al.*, 1995; *Kurz and Apps*, 1995].

We used field studies of C input, storage, and turnover in the northern region of the boreal forest, made as part of the BOReal Ecosystem-Atmosphere Study (BOREAS), to develop simple models linking soil C storage and rates of accumulation to two major factors: soil drainage class and the time since last fire [*Trumbore and Harden*, 1997; *Harden et al.*, 1997]. These models have previously been combined with a soil drainage map for a 120 year old black spruce stand to compare the soil component of net C storage with tower-based, eddy covariance measurements of net ecosystem production [*Harden et al.*, 1997]. In this paper, we expand this scaling approach to

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estimate the soil C storage and accumulation rates for a 733 km^2 area within the BOREAS Northern Study Area (NSA), in northern Manitoba, Canada. More specifically, we (1) estimate total C stocks by horizon for common soil series on the basis of soil survey data and analyses of data from individual soil profiles; (2) estimate rates of soil C accumulation on the basis of C stocks and a simple model of C turnover derived from field radiocarbon studies; (3) relate patterns of C stocks and accumulation rates to patterns of drainage, moss cover, and fire history; and (4) generate area-weighted maps of soil C stocks and accumulation rates across the 733 km^2 study area in 1994, the year in which most BOREAS field studies were conducted. We also identify areas of greatest sensitivity and uncertainty in these estimates.

2. Methods and Data Sources

2.1. Study Area

The BOREAS Northern Study Area, located between Thompson and Nelson House, Manitoba, is near the northern limit of the closed-crown boreal forest (Figure 1a) [*Sellers et al*, 1994]. We focus here on a 733 km^2 study area within the NSA (Figure 1b), for which a soil survey map was generated during the 1994 BOREAS field season [*Veldhuis and Knapp,* 1998b]. Corner coordinates of the study area are: 56.00°N, 98.69°W; 56.00°N, 98.17°W; 55.80°N, 98.18°W; 55.80°N, 98.69°W.

Much of the region is underlain by poorly drained, varved clay deposited by Glacial Lake Agassiz and interspersed with frequent bedrock outcrops. A few minor exposures of well-

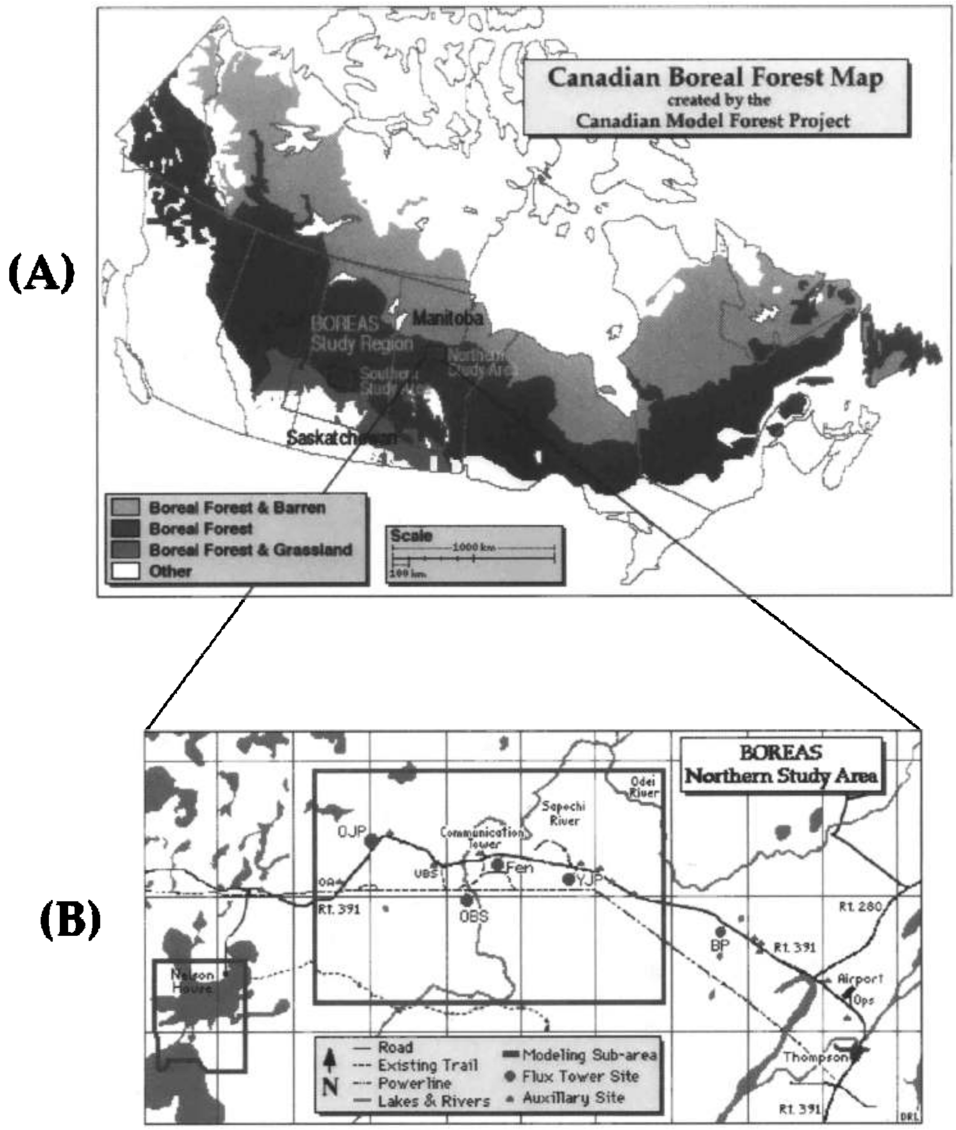


Figure 1. (a) Map of Canadian boreal forests showing the BOREAS study region and the northern and southern sites and (b) map of BOREAS Northern Study Area. The 733 km^2 study area is drawn in black. The eddy flux tower sites are: Old Jack Pine (OJP), Old Black Spruce (OBS), Fen (FEN), Young Jack Pine (YJP), and Beaver Pond (BP). These maps were modified from those publicly available courtesy of BOREAS (http://boreas gsfc nasa gov)

drained, sandy glacial till occur, largely in the eastern part of the study area, where two major hills composed of sand and gravel (kame deposits) run north-south with relief up to 60 m [*Sellers et al.*, 1994]. (See Figure 2a and Plate 1b.) Extensive areas of the clayey deposits are overlain by deep and shallow organic deposits (peat). Permafrost occurs sporadically and at variable depths in clayey upland soils and in veneer bogs [*Sellers et al.*, 1994; *Rubec*, 1988; *Veldhuis and Knapp*, 1998b], and is continuous in collapse scar and peat plateau bogs and palsas [*Rubec*, 1988; *Veldhuis and Knapp*, 1998b]. The area is undulating with long gentle slopes. Forest stand ages range from 13 to 140 years or more on uplands, marking the period elapsed since the last fire.

Stratifying the study area by drainage class is an effective means of identifying land cover type. We identified six broad land cover types on the basis of similarities in landform, drainage, depth of organics (peat), and dominant forest and moss cover. In the following descriptions, the Canadian soil classification [*Agriculture Canada Expert Committee on Soil Survey*, 1987] is followed (in parentheses) by the U.S. classification [*Soil Survey Staff*, 1975, 1996 (also available on the World Wide Web at http://www.statlab.iastate.edu/soils/ keytax/)]: (1) upland, well-drained, sandy Eluviated Dystric Brunisols (Cryochrepts) with jack pine (*Pinus banksiana*) cover; (2) upland, moderately well-drained, clayey Orthic Gray Luvisols (Cryoboralfs) with mixed black spruce (*Picea mariana*) and hardwood stands with feather moss (*Pleurozium, Hylocomium* spp.) as the dominant ground cover; (3) transitional, imperfectly to poorly drained, clayey Gleyed Gray Luvisols and Luvic Gleysols (Cryoboralfs) with black spruce and a mixture of feather and sphagnum (*Sphagnum* spp.) mosses; (4) poorly to very poorly drained, level to gently sloping, clayey, peaty Luvic Gleysols and Terric Mesic Fibrisols (Cryoboralfs and Cryofibrists) with black spruce and sphagnum moss mixed with feather and other mosses; (5) peatlands consisting of varying peat materials that are well- to poorly drained at the surface and have frozen peat and/or mineral material at depth, with Fibric and Mesic Organic Cryosols (Cryofibrists and Cryohemists), and black spruce and sphagnum/feather moss vegetation cover. (Palsas are mounds of upland peatlands underlain by perennially frozen peat and mineral soil, with rough and uneven surfaces, and are characterized by having domed surfaces. Peat plateau bogs, also underlain by continuous permafrost, rise abruptly from surrounding unfrozen fens and are characterized by having relatively flat and even surfaces [*Rubec*, 1988; *Veldhuis and Knapp*, 1998b]); and (6) very poorly drained fens and permafrost collapse bogs with deep Typic Fibrisols (Cryofibrists), and sedge and brown moss vegetation. (Fens are wetlands fed by groundwater that is relatively nutrient rich (compared to precipitation), whereas bogs are oligotrophic, having their upper peat layer (rooting zone) above the groundwater flow, and therefore have a rooting zone largely dependent on precipitation for its water and nutrient supply. Vegetation of the fens is characteristically sedge (*Carex, Eriophorum* spp.) and brown moss (*Depranocladus, Tomenthypnum* spp.). Sphagnum and/or feather mosses occur in bogs. Collapse scar bogs are nutrient poor circular or oval depressions caused by subsidence of the peatland surface due to thawing of permafrost [*Rubec*, 1988; *Veldhuis and Knapp*, 1998b]).

In addition to soil drainage, the incidence of fire is an important factor controlling annual accumulation rates of soil C [*Bonan*, 1993; *Moore and Knowles*, 1990; *Gorham*, 1991; *Kasischke et al.*, 1995; *Kurz and Apps*, 1995]. A 1981 fire burned about 128 km^2 of the predominantly spruce-forested southern part of the study area. (See Plate 1a.) Smaller burns totaling about 33 km^2 occurred in 1956 and 1964 along the north-south ridge near the eastern boundary where primarily jack pine has regenerated. In 1989, large areas burned in the western and northern sections of the NSA, outside of the study area. None of the study region burned in 1994.

2.2. Soil C Storage

Models of soil C dynamics were developed using data on C inventories and radiocarbon as part of the BOREAS field effort [*Trumbore and Harden*, 1997; *Harden et al.*, 1997]. Upland soil profiles were divided into two layers (Figures 2a and 2b) that are distinctly different in their C dynamics: (1) a surface detrital or moss layer, made up of relatively undecomposed organic material, and (2) a deep layer consisting of more highly decomposed organic matter (humic layer), in which plant macrofossils are rare, and where minor amounts of organic matter are incorporated into the mineral soil A horizon. The mineral B horizon was also included in this deep layer.

2.2.1. Upland surface soil layers. Upland surface layers accumulate C between fire events. Organic C is input directly to the surface layer as detritus from trees and mosses. Decomposition rates are generally slow (mean residence times of the order of decades), so that thick organic mats accumulate in shallow layers before losses through decomposition offset annual additions. Feather moss cover on moderately well- to imperfectly drained soils tends to dry out in summer because it does not overlie saturated soils and hence will burn nearly completely to mineral soil in stand-killing fires. In contrast, sphagnum moss cover is associated with imperfectly and poorly drained soils that tend to stay moist at depth and therefore burn less completely.

We modeled soil C accumulation of the surface layers between fires as a simple balance of C inputs and first-order decomposition using the following equations from *Jenny et al.* [1949] and *Harden et al.* [1992, 1997]:

$$dC/dt = I - (k \times C) \tag{1}$$

Solving for C in Equation (1) yields:

$$C(t) = I/k \times (1 - e^{-kt}) \tag{2}$$

where C is carbon mass in units of mass per area, t is number of years since the last stand-killing fire, I is input rate in mass per unit area per year, and k is a decomposition coefficient in units of years^{-1}.

Input I rates and decomposition k constants (Table 1) were determined using two approaches. First, vertical accumulation rates of moss were obtained using radiocarbon analyses to determine the age of accumulated C [*Trumbore and Harden*, 1997]. Second, surveys of the C inventory in organic matter above the most recent charcoal layer in the soil profile were made across a series of sites (chronosequence) that differed in time since last fire [*Harden et al.*, 1997]. The estimates of I and k based on chronosequences were used for upland sites with feather and sphagnum mosses on clay parent material to

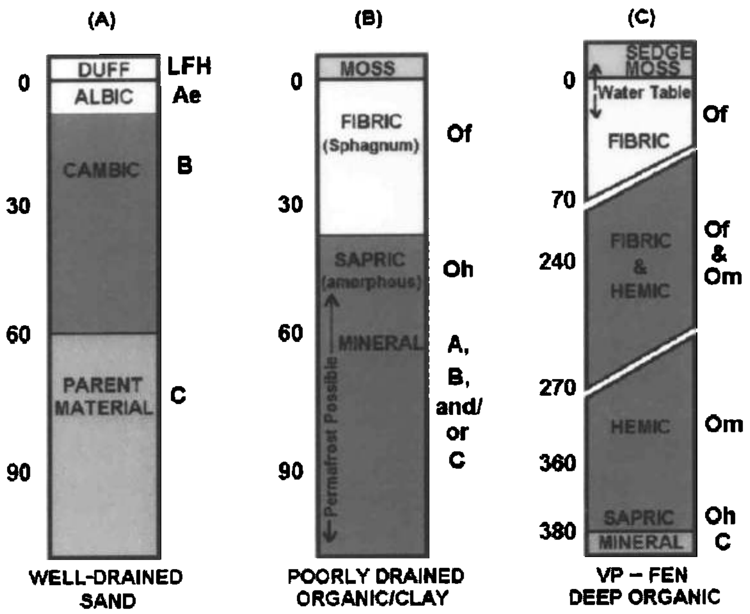


Figure 2. Typical boreal forest soil profiles from three sites: (a) well-drained sand, (b) poorly drained organic materials and clay soil, and (c) very poorly drained fen with deep organic material. Profile depths are in centimeters. Soil profile nomenclature is from the *Agriculture Canada Expert Committee on Soil Survey* [1987] and *Soil Survey Staff* [1975, 1996].

represent both vertical and lateral accumulation of moss [*Harden et al.*, 1997]. The radiocarbon-derived *I* and *k* values were used for jack pine sites on sandy soils and for wetlands, where no chronosequence data were available.

Although the various components of litter layers, such as leaves, moss, and roots, decompose at different rates, the use of a single *k* value does a reasonable job of describing the decadal process of accumulation of C in regrowing moss and detritus in the BOREAS Northern Study Area [*Trumbore and Harden*, 1997; *Harden et al.*, 1997]. The majority of the mass of C in the slow-growing detrital layer is dead moss, and the *k* values derived from field studies largely describe decomposition of moss rather than the other litter components, which constitute a smaller fraction of the total C in the layer and which do not continue to accumulate substantially over decades.

This model assumes that the C stock in surface moss and detritus is zero immediately following fire and that input rates and decomposition constants do not change over time as moss layers regrow and accumulate C after fire. *Harden et al.* [1997] found that allowing the value of *k* to change with time did not significantly improve the fit to chronosequence data over that of a fixed *k* value.

2.2.2. Upland deep soil organic layers. The deep soil layers are composed of decomposed organic matter and the mineral A and B horizons. In contrast to the surface layers, which are made up of recognizable plant fragments, deep soil organic matter consists of humified material (dark-colored organic matter not associated with minerals in which pieces of moss and litter are no longer identifiable), charcoal, and mineral-associated C. The deep soil C is derived from organic matter that was originally added as surface detrital and moss layers but was later transferred to deep organic layers through the accumulation of charred remnants of fires and the downward percolation of soluble organic material Radiocarbon measurements show that most of the C in the deep organic layers has turnover times of centuries or millennia [*Trumbore and Harden*, 1997] and that these layers have accumulated slowly, influenced by many fire events over the millennia since the drying of Glacial Lake Agassiz. Input *I* and decomposition *k* rates used for deep soil layers (Table 1) were derived using the accumulation of C and ^{14}C since deglaciation [*Trumbore and Harden*, 1997].

We made the assumption that deep C pools in upland soils gain C immediately following fire and experience net C loss between fire events through decomposition [*Harden et al*, 1997]. One exception to this assumption was made for the jack pine sites, where *Trumbore and Harden* [1997] found radiocarbon in the deep sandy soils from atmospheric thermonuclear weapons testing during the 1950s and 1960s. Hence C inputs must have occurred to these soil horizons during the last 30 years, probably from sources other than fire residues, such as inputs of C from pine roots and inputs from dissolved organic carbon.

2.2.3. Wetland soils. Wetland soils can also be split into two layers with distinctly different C dynamics [*Clymo*, 1984]: (1) the surface layers, which include the acrotelm (the aerobic portion of the soil profile above the water table) and the upper portion of the catotelm (the submerged, anaerobic portion below the water table) where organic material is still recognizable, and (2) the deep horizons of the catotelm where organic matter is more decomposed (Figure 2c).

The surface layer of the wetland can dry out or grow above the water table. Decomposition rates of mosses in this upper zone are comparable to those in upland surface layers (Table 1). For fens and collapse scar bogs, we assume that the surface layer is at steady state and that any C not decomposed is pushed below the water table to be added to the deeper layers.

Trumbore and Harden [1997] found that the inventory of the

Table 1. Input I and Decomposition k Constants for Surface and Deep Soil Layers

Soil Horizon	Drainage Class	I, kg C m^{-2} yr^{-1}	k, yr^{-1}
Surface	Well	0.06	0.07
	Moderately well	0.08	0.013
	Imperfect	0.07	0.0105
	Poor		
	Sphagnum moss	0.06	0.008
	Palsa	0.08	0.013
	Very poor		
	Fen	0.0324[a]	0.02[a]
	Collapse scar bog	0.0324[a]	0.02[a]
Deep	Well	0.015	0.01
	Moderately well	0	0.003
	Imperfect	0	0.002
	Poor		
	Sphagnum moss	0	0.0007
	Palsa	0	0
	Very poor		
	Fen	0.064	0.0004
	Collapse scar bog	0.064	0.0004

Information in this table is from *Trumbore and Harden* [1997].

[a] These values are fixed for a C inventory of 13 kg C m^{-2}, so as to give 0.064 kg C m^{-2} yr^{-1}, the input to the deep layers.

surface layers of fens ranged from 6 to 13 kg C m^{-2}. For this study, we chose the inventory of the surface layer to be 13 kg C m^{-2}, because this is the C inventory required to calculate the observed deep input value of 0.064 kg C m^{-2} yr^{-1}, using surface values of I and k given in Table 1 (and $I_{\text{deep}} = I_{\text{surface}} - (k_{\text{surface}} \times C_{\text{surface}})$). This inventory corresponds to a depth of approximately 70 cm (Figure 2c), where the organic matter is visibly more decomposed and where bulk density increases. The top 70 cm increment includes C that has been fixed over roughly the last 50-100 years [*Trumbore and Harden*, 1997].

Below the water table, oxygen limitation slows decomposition rates [*Clymo*, 1984]. Unlike upland soils, where inputs to the deep soil are tied to fire, C is added continuously to deep layers of wetlands as the growing surface layer of moss pushes organic matter below the water and as the water table rises with the accumulation of the peat material. Decomposition in the deep wetland soils is affected by surface drainage and the presence or absence of permafrost. Carbon inputs and decomposition coefficients (Table 1) were determined from radiocarbon analyses and C inventory data for both surface and deep layers [*Trumbore and Harden*, 1997]. For the palsas and peat plateau bogs, we set deep decomposition rates to zero, because these layers are frozen solid year-round. Wetlands burn only infrequently, typically down to the water table.

2.3 Spatial Data

The spatial base for our analyses is a soil polygon map [*Veldhuis and Knapp*, 1998b] from an extensive and detailed soil survey of the 733 km^2 study area. The map is at 30 m resolution, in raster form, and uses the BOREAS grid coordinate system (on the basis of the Albers Equal-Area Conic projection) in the 1983 North American Datum (NAD83). Accompanying the soil polygon raster image is an attribute table that describes in detail each component of each respective soil polygon. Spatial variation is indicated by estimates of the percent area of the total polygon occupied by the dominant soil series and each of the minor soil series inclusions within each map polygon.

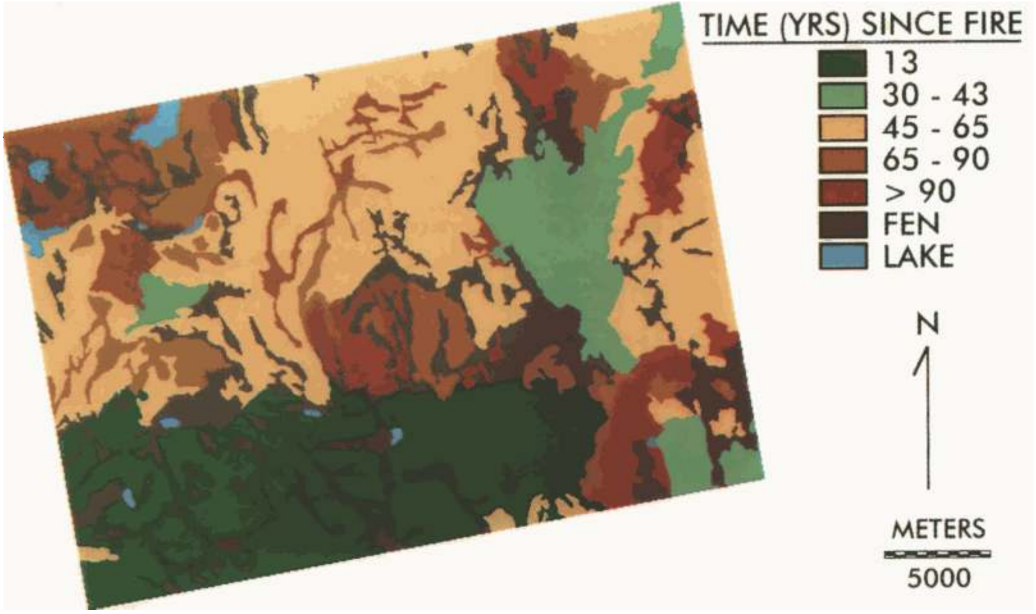
2.3.1. Map of forest stand age. Using a classified Landsat Thematic Mapper image from August 20, 1988 [*Hall and Knapp*, 1998], we identified the burn scar of the large 1981 fire that encompassed most of the southwest portion of the study area. The perimeter of the regeneration area was screen-digitized and overlaid onto the soil polygon map. Using 1994 as the base year, we assigned a stand age of 13 years to those polygons and portions of polygons within the 1981 burn. We assumed any inclusion classified as a fen or collapse scar bog did not burn in this or any other fire.

From the Canadian Forest Service series of hand-drawn fire maps dating back to the 1930s, we determined approximate locations of the major burns of 1956 and 1964. We then used digital maps from the Natural Resources Manitoba (NRM) 1988 forest inventory, which includes data layers of species cover, cutting class, and site class (which includes age ranges for the three major forest cover types) [*Knapp and Tuinhoff*, 1998]. We then generated a data layer that assigned an age or age range for each forest stand. These data layers were then used to isolate 30 to 40 year old upland jack pine stands that occupy the north-south ridge in the eastern portion of the study area and that correspond to the sites identified in the hand-drawn Canadian Forest Service fire maps as the 1964 and 1956 burns.

For areas along Highway 391 (see Figure 1b), which essentially is an east-west transect through the study area, we used tree core data collected in the *Halliwell and Apps* [1996] extensive biometric survey of the BOREAS Northern Study. The *Halliwell and Apps* [1995] tie-in points were overlaid with the soil polygon map, and a mean forest stand age was calculated for each relevant polygon. Where cores were taken at breast height, we added 10 years for spruce and 5 years for jack pine and aspen (G. Peterson, personal communication, 1997) to the number of recorded rings.

To estimate stand ages for the remaining areas where there were neither fire scars nor tree core data, we relied on the ranges of stand ages reported in the Natural Resources Manitoba (NRM) 1988 forest inventory [*Knapp and Tuinhoff*, 1998]. Noting that the more site specific ages derived from the fire scar and tree core data were at the high end of the age ranges reported in the 1988 NRM inventory, we used the high end of the NRM age ranges for all other areas. For areas that were not

(A) FOREST STAND AGE



(B) SOIL DRAINAGE

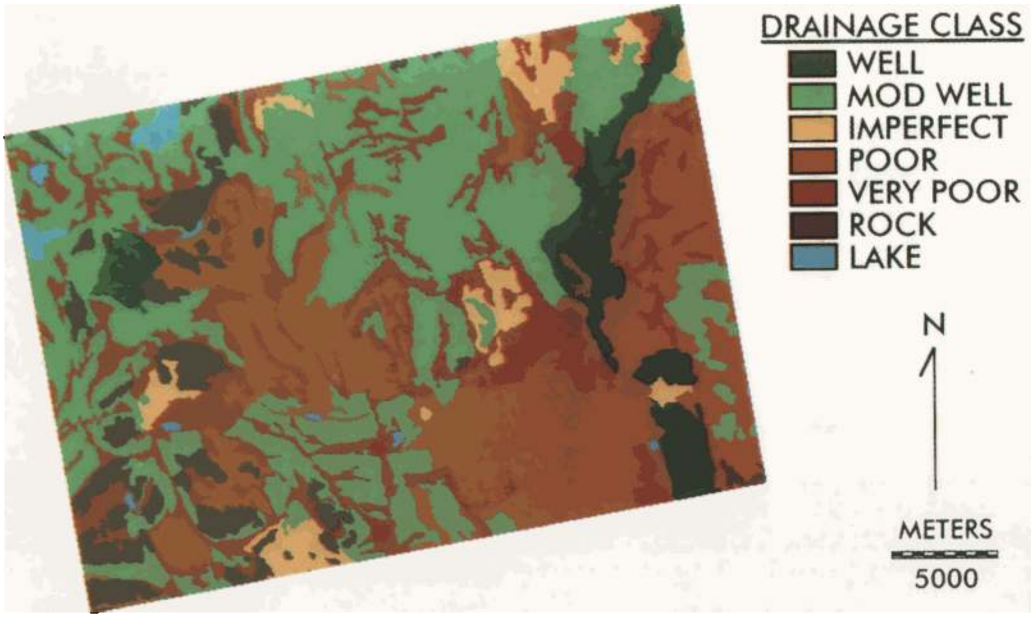
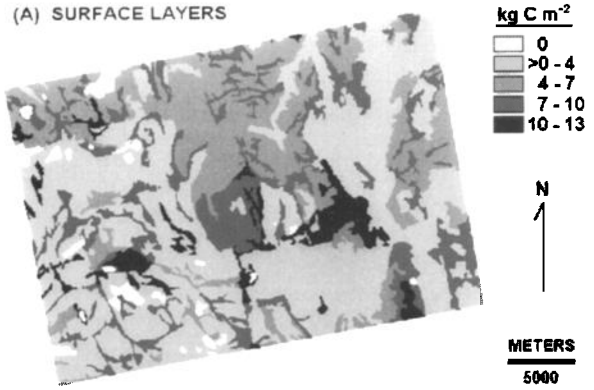


Plate 1. (a) Forest stand age map of 733 km^2 study area compiled from satellite images, fire maps, forest inventory, and tree core data. Age ranges represent time since last fire. The reference year is 1994. Fens are those soil polygons from the *Veldhuis and Knapp* [1998b] soil survey for which 50% or more of the area is classified as fen and/or collapse scar bog and is assumed not to have burned. (b) Soil drainage map of 733 km^2 study area. The map represents soil drainage by dominant soil series of soil polygons from the *Veldhuis and Knapp* [1998b] soil survey.

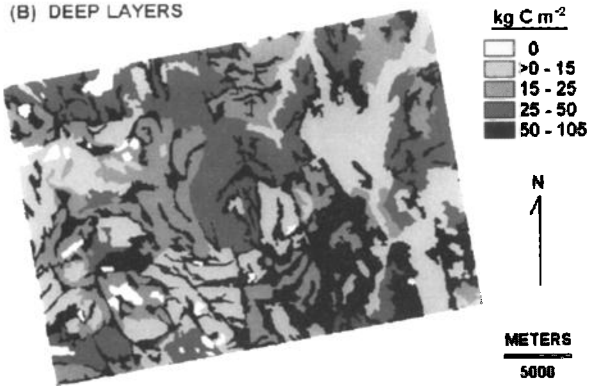
inventoried in the 1988 NRM survey, because of their unproductive wetland status, we assumed stand ages were the same as contiguous stands with similar characteristics for which data were available.

The resulting forest stand age map (Plate 1a) was used for model input. Finite ages were assigned to the burned areas. We assumed that fires occur infrequently in fens and collapse bogs and did not assign stand ages. For all other polygons, a range of probable ages was determined, and the midpoint of that range was used for model input for each inclusion of each soil polygon.

(A) SURFACE LAYERS



(B) DEEP LAYERS



(C) TOTAL PROFILE

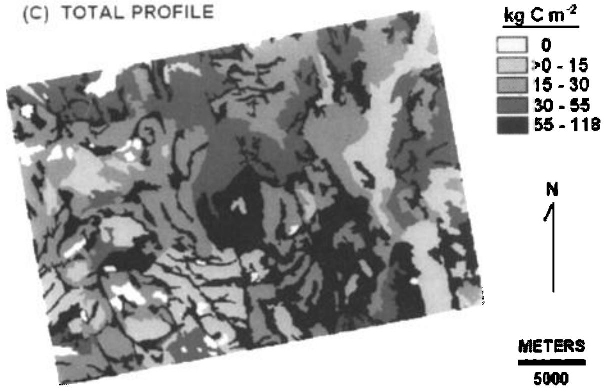


Figure 3. Soil carbon stocks of the 733 km^2 study area. The maps represent area-weighted averages of (a) surface layers, including moss, (b) deep layers, and (c) total profile. Depths varied among soil series. See text for discussion of surface and deep layers.

2.3.2. Map of soil drainage. The soil drainage map (Plate 1b) represents the drainage class of the dominant soil series of each soil polygon, using data collected in the soil survey [*Veldhuis and Knapp,* 1998b]. Not shown on this map are the minor inclusions of other soil series within each polygon, but these accompanying data on the spatial extent of each soil series that was used in model calculations are described below.

2.3.3. Carbon stock maps. For generating the soil C stock maps (Figure 3), we followed the methods outlined by *Davidson* [1995] and *Davidson and Lefebrve* [1993], with a few adaptations to account for differences in the BOREAS data sets. By employing area-weighted estimates for soil polygons and numerically accounting for minor inclusions of unnamed soil series within each named soil polygon, soil series are included that are relatively unimportant spatially but that may make significant contributions to soil C stocks [*Davidson and Lefebrve,* 1993].

Data from soil pits were not used to calculate soil C stock of the surface layers, because the depth of the surface layers is influenced more by time since the last fire than it is a characterization of a given soil series. Instead, surface layer C stocks (kg C m^{-2}) were calculated for each fractional component (i.e., soil series inclusion) of each soil polygon, using I and k values appropriate to each drainage class (Table 1) and t values from the forest stand ages of the fire history map (Plate 1a). [See also *Rapalee et al.,* 1998.] The area-weighted averages for each polygon were then mapped (Figure 3a).

The average deep soil C inventory for each soil series was calculated from field observations of bulk density and C content made by *Trumbore et al.* [1998] and *Veldhuis and Knapp* [1998a] for humic and mineral horizons (below the layer of charred material). These averages were used to calculate area-weighted deep C stocks for each polygon (Figure 3b). For about 12% of the study area where no data were available for the soil series, we used the average C inventory for deep soils from similar soil series.

Because many soil profile descriptions had missing data on bulk density (BD), we developed nonlinear regressions relating bulk density to C content for the soil profile descriptions that had both. Several published regressions for predicting bulk density from C concentrations [*Huntington et al.,* 1989; *Curtis and Post,* 1964; *Alexander,* 1989] could not be used because our data set included organic soils with high C content and mineral soils with very low C content (<1%), which extend beyond the valid range of these reported regressions. We derived the following regressions (see Figure 4):

Veldhuis and Knapp [1998a]:

$$\ln(\mathrm{BD}) = 0.271 - 0.066 \times \%\mathrm{C} \qquad (R^2 = 0.91) \qquad (3)$$

Trumbore et al. [1998]:

$$\ln(\mathrm{BD}) = 0.132 - 0.072 \times \%\mathrm{C} \qquad (R^2 = 0.77) \qquad (4)$$

Missing bulk density data for horizons of soil series in both datasets were estimated from these equations. Carbon stocks of

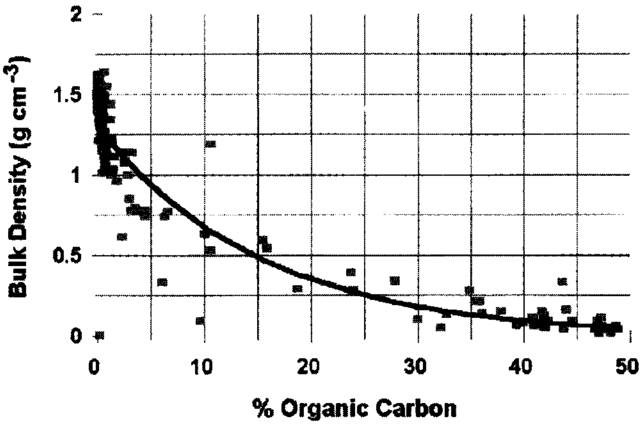


Figure 4. Bulk density (BD) versus percentage of carbon for all soil horizons of the *Veldhuis and Knapp* [1998a] data set where: ln(BD) = 0.271 − 0.066 × %C. $R^2 = 0.91$.

each deep horizon of each profile were calculated by multiplying bulk density by percent C and depth, and the products were summed for each deep soil series profile, including B horizons, when present [*Davidson and Lefebvre*, 1993]. Soil depth varied among soil series from 23 cm for the most shallow sandy soil profile to 495 cm for the deepest reported profile of a bog soil [*Veldhuis and Knapp,* 1998a]. The average C content of each soil series was multiplied by the percent area of the polygon covered by the respective soil series, and these products were summed for the each polygon, providing an area-weighted estimate of deep soil C stocks for each polygon (Figure 3b).

3. Results

3.1. Spatial Distribution

The study site is a mosaic of drainage classes and forest stand ages, with no one class comprising more than 28% of the area (Table 2). About one quarter of the total area is 43 years old or younger, having burned in 1956 and 1964 (10%) and in 1981 (18%). Another 28% is within the 45-65 year range and 6% in the 65-90 year range. Only 11% of the total area is greater than 90 years old, mostly at the BOREAS NSA Old Black Spruce (OBS) tower site. (See Figure 1b and Plate 1a.)

Black spruce is the dominant forest cover, occupying 53% of the landscape. About half of the black spruce occurs in the 45-65 year age class, and the rest is distributed throughout the other age classes. Of the area dominated by black spruce, 21% is moderately well-drained with feather moss ground cover, 20% is poorly drained with sphagnum moss, and 12% is imperfectly drained with a mixture of sphagnum and feather mosses. In contrast, jack pine occupies about 6% of the total area, which is well-drained and mostly in the 30-43 year age range along the north-south ridge in the eastern section that burned in 1956 and 1964 (Plate 1b).

Wetlands and palsas occupy about one third of the total area.

Table 2. Percent of Total Study Area by Forest Stand Age and Land Cover Type

	Time Since Fire, years					
	13	30-43	45-65	65-90	>90	Total
Well						
Jack pine	0	5	< 1	0	1	6
Moderately well						
Black spruce/Feather moss	5	2	10	2	2	21
Imperfect						
Black spruce/Mixed mosses	3	1	6	1	1	12
Poor						
Black spruce/Sphagnum moss	4	2	9	2	3	20
Palsa	6	< 1	3	1	4	14
Very poor						
Fen						18
Collapse scar bog						1
Other						
Rock, water, lake						8
Total	18	10	28	6	11	100

Poorly drained palsas cover 14% of the study area, about half of which is within the 1981 burn (Plate 1a). The very poorly drained fens and collapse scar bogs cover 18% of the total area, distributed in low-lying areas throughout the study area (Plate 1b).

3.2. Soil Carbon Stocks

Moss and surface soil C stocks vary with forest stand age and drainage class, with lowest stocks in the well-drained, recently burned sites and highest in the very poorly-drained and unburned wetlands (Figure 3a and Table 3). Averaged over the entire study area, surface layer C stocks are 4 kg C m^{-2}, but variability ranges from 13 kg C m^{-2} for very poorly drained fens and collapse bogs to 3 kg C m^{-2} as the mean for uplands.

The bulk of C is stored in the deep soil layers (Figure 3b), with C inventory ranging from 3 kg C m^{-2} in well-drained jack pine stands to 88 kg C m^{-2} in the very poorly drained fens and 131 kg C m^{-2} in the collapse scar bogs, with an average of 37 kg C m^{-2} for the entire study area (Table 3). Deep C inventory is controlled by drainage class and is unaffected by recent fire history. Area-weighted averages of deep C stock in each drainage class vary only slightly among their respective age ranges (Table 3). This is in contrast with surface C stocks, which are lowest shortly after fire and increase as the forest stands age. In the imperfectly-drained sites, for example, deep C stocks are 20 and 19 kg C m^{-2} in the 13 and >90 year sites, respectively, but the surface C stock at the same sites increases from 1 to 5 kg C m^{-2}, respectively.

Total soil C stocks covary with drainage classes and are dominated by the deep soil layers, with the largest C stocks occurring in the more poorly drained sites (Figure 3c). Although the very poorly drained fens and collapse scar bogs together occupy only about one fifth of the total area, they account for a little over half of the total C stocks (Table 3). Poorly drained palsas cover 14% of the landscape and account for 26% of total C stocks. The entire 733 km^2 study area stores 3 × 10^{12} g C in the surface soil layers and 25 × 10^{12} g C in the deep layers, for a total of 28 × 10^{12} g C.

3.3. Rates of Soil Carbon Accumulation and Loss

Rates of C accumulation in surface layers were calculated using (1), with I and k values from Table 1 for the forest stand ages and six drainage class types from Plates 1a and 1b. [See also *Rapalee et al.*, 1998.] Calculated annual accumulation in the surface layers ranges from an average of 64 g C m^{-2} yr^{-1} in the 1981 burn site to 21 g C m^{-2} yr^{-1} in sites older than 90 years, with an average of 28 g C m^{-2} yr^{-1} for the entire study site (Table 3, Figures 5a and 6a). Not shown in Figure 6a are the fens and collapse scar bogs, where surface C stocks are assumed to be at steady state (zero net accumulation). In the uplands, forest stand age influences surface C accumulation rates more than does soil drainage (Figure 6a).

Rates of deep soil C net losses and accumulations were calculated in the same way as for surface layers (equation (1)), but with the I and k values for inputs and decomposition constants for the deep layers indicated in Table 1. Modeled net deep soil C losses for the entire 733 km^2 study area are 9 g C m^{-2} yr^{-1} (Table 3). Losses for upland deep soils range from 0 in the frozen palsas to about 40 g C m^{-2} yr^{-1} from imperfectly drained soils (Figures 5b and 6b). Although decomposition rates are faster in the moderately well-drained upland soils, the C inventory is lower, so losses are smaller than for imperfectly drained soils. For poorly drained soils, decomposition rates are very slow (Table 1), so that loss rates are low even though C inventories are large.

Losses of C from the deep soil of uplands in years between fire events partly cancel the rate of accumulation of C in the upper moss layers, resulting in a net change of nearly zero for the entire soil-moss profile. Net accumulation of soil C in the total profile depends on both drainage class and time since last fire, with the largest rates of soil C accumulation in fens and in the surface mosses of recently burned sites (Figure 5c).

In the fens and collapse scar bogs, deep soil layers are accumulating, because the input values (I) exceed losses ($k \times$ C; equation (1)). The model estimates that the fens are storing on average 28.8 g C m^{-2} yr^{-1} in deep layers (Table 3), which agrees with commonly reported accumulation rates of 29 g C m^{-2} yr^{-1} in undrained and unmined boreal and subarctic peatlands [*Gorham*, 1991].

These results indicate that the study area was a small net sink of atmospheric C in 1994, with gains in regrowing surface moss layers partly offset by decomposition in deep, humic soil layers. Estimated rates of net C accumulation are 20 g C m^{-2} yr^{-1} averaged over the 733 km^2 study area, and they sum to 15 × 10^9 g C for the entire study area (Figure 7 and Table 3). Most of the accumulation occurs in the poorly drained black spruce-sphagnum moss sites, the palsas, and the very poorly drained fens and collapse scar bogs (Figure 7).

3.4. Sensitivity Analyses

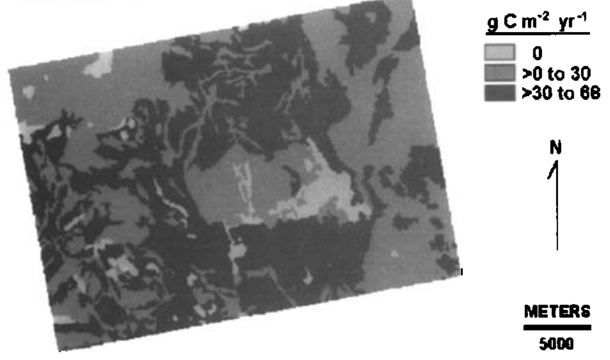
We tested the sensitivity of the modeled soil C dynamics to two factors: (1) the assigned values for deep soil decomposition constants (k) and (2) the estimates of forest stand age, as these are the two inputs to the model with the greatest uncertainty. The first test compared results of using a range of deep layer decomposition constants, including the "reference case" of values reported in Table 1 and high and low k values that are within the ranges reported by *Trumbore and Harden* [1997] to be consistent with their radiocarbon data (Table 4). Changes in deep soil C averaged over the entire area ranged from a small accumulation (+5 g C m^{-2} yr^{-1}) using the lowest k values to a loss (-22 g C m^{-2} yr^{-1}) using the highest k values. The calculated deep soil C loss using the high k values is large enough to almost completely counter the surface layer sink (Table 4). These results highlight the potential importance of deep soil C in the net budget of the system and the importance of narrowing uncertainties in the estimates of deep soil C decomposition rates.

The second sensitivity analysis estimated changes in annual soil C accumulation rates if the entire study area (except fens and collapse scar bogs) had burned 13, 30, 60, and 120 years ago (Table 5). In effect, each of these simulations assumes that the 1981 fire, the 1964 fire, and two older fires, which correspond to average stand age and the age of the Old Black Spruce tower site, had each uniformly burned the entire study area. Rates of simulated surface layer accumulation rates are 46 g C m^{-2} yr^{-1} in the scenario where the entire site burned 13 years ago and decrease to 14 g C m^{-2} yr^{-1} at 120 years after fire (Table 5). Using a uniform stand age of 120 years, the total calculated C accumulation is near zero (5 g C m^{-2} yr^{-1}), with release of C by the deep layers (-9 g C m^{-2} yr^{-1}) nearly offsetting uptake by the surface layers (14 g C m^{-2} yr^{-1}).

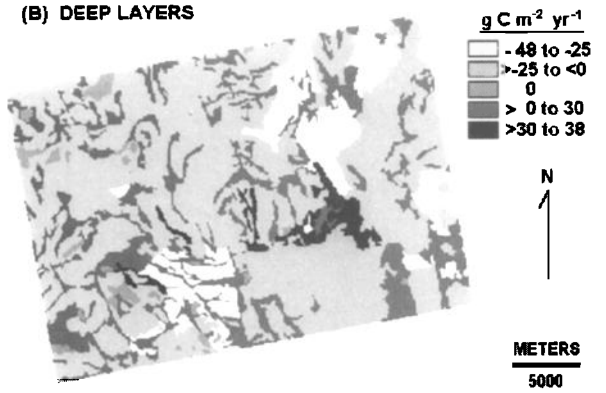
Table 3. Areal Coverage, Organic Carbon Stocks, and Rates of C Accumulation and Loss by Drainage Class, Vegetation Type, and Age Class for 733 km^2 Study Site Within the BOREAS Northern Study Area

Drainage Class	Vegetation Type	Age Class	Study Area		C Stock Area-Weighted Average, kg C m^{-2}			C Stock Total for Study Area, 10^{12} g C				C Accumulation/Loss Area-Weighted Average, g C m^{-2} yr^{-1}			C Accumulation/Loss Total for Study Area, 10^9 g C yr^{-1}		
			km^2	%	Surface	Deep	Total	Surface	Deep	Total	Total, %	Surface	Deep	Total	Surface	Deep	Total
Well	Jack pine	13	0	0.0	0.0	0.0	0.0	0.00	0.00	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		30-43	33	4.5	0.8	2.8	3.6	0.03	0.09	0.12	0.4	6.6	-13.1	-6.4	0.2	-0.4	-0.2
		45-65	2	0.3	0.8	3.7	4.6	0.00	0.01	0.01	<0.1	0.9	-22.2	-21.3	<0.1	-0.1	<0.0
		65-90	0	0.0	0.0	0.0	0.0	0.00	0.00	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		>90	11	1.4	0.9	3.1	4.0	0.01	0.03	0.04	0.1	0.1	-16.0	-15.9	0.0	-0.2	-0.2
Moderately well	Black spruce	13	37	5.0	1.0	9.6	10.6	0.04	0.35	0.39	1.4	67.6	-28.8	38.7	2.5	-1.1	1.4
	Feather moss	30-43	12	1.7	2.1	12.7	14.8	0.03	0.16	0.18	0.7	52.8	-38.0	14.8	0.7	-0.5	0.2
		45-65	71	9.6	3.3	11.0	14.3	0.24	0.78	1.01	3.6	36.7	-32.9	3.8	2.6	-2.3	0.3
		65-90	12	1.7	3.7	11.6	15.3	0.04	0.14	0.19	0.7	32.2	-34.9	-2.7	0.4	-0.4	< 0.0
		>90	15	2.1	4.4	9.8	14.2	0.07	0.15	0.22	0.8	22.7	-29.5	-6.8	0.4	-0.5	-0.1
Imperfect	Black spruce	13	21	2.8	0.8	19.6	20.4	0.02	0.41	0.43	1.5	60.8	-39.2	21.7	1.3	-0.8	0.5
	Mixed mosses	30-43	6	0.8	1.9	15.6	17.5	0.01	0.09	0.10	0.4	49.7	-31.2	18.5	0.3	-0.2	0.1
		45-65	46	6.2	3.1	19.7	22.8	0.14	0.90	1.05	3.7	36.9	-39.5	-2.6	1.7	-1.8	-0.1
		65-90	8	1.1	3.4	15.3	18.7	0.03	0.13	0.16	0.6	33.2	-30.6	2.6	0.3	-0.3	0.0
		>90	8	1.1	4.8	19.4	24.2	0.04	0.16	0.20	0.7	25.3	-38.9	-13.6	0.2	-0.3	-0.1
Poor	Black spruce	13	26	3.6	0.7	11.7	12.5	0.02	0.31	0.33	1.2	54.1	-8.2	45.9	1.4	-0.2	1.2
	Sphagnum moss	30-43	14	1.9	1.7	14.1	15.8	0.02	0.20	0.22	0.8	46.5	-9.8	36.7	0.7	-0.1	0.5
		45-65	68	9.3	2.9	12.0	14.9	0.19	0.82	1.01	3.6	37.1	-8.4	28.7	2.5	-0.6	2.0
		65-90	12	1.6	3.2	11.7	15.0	0.04	0.14	0.18	0.6	34.3	-8.2	26.1	0.4	-0.1	0.3
		>90	24	3.3	4.2	14.3	18.4	0.10	0.35	0.45	1.6	26.7	-10.0	16.7	0.7	-0.2	0.4
Poor	Palsa	13	44	6.0	1.0	69.9	70.9	0.04	3.06	3.10	11.0	67.6	0.0	67.6	3.0	0.0	3.0
		30-43	<1	<0.1	2.6	55.9	58.5	<0.01	0.01	0.01	0.1	45.7	0.0	45.7	<0.1	0.0	<0.1
		45-65	23	3.1	3.3	60.8	64.1	0.08	1.39	1.47	5.2	36.7	0.0	36.7	0.8	0.0	0.8
		65-90	8	1.1	3.7	65.3	68.9	0.03	0.51	0.54	1.9	32.2	0.0	32.2	0.3	0.0	0.3
		>90	31	4.2	4.8	70.3	75.1	0.15	2.16	2.31	8.2	21.6	0.0	21.6	0.7	0.0	0.7
Very poor	Fen	N/A	131	17.9	13.0	88.0	101.0	1.7	11.6	13.3	47.0	0.0	28.8	28.8	0.0	3.8	3.8
	Collapse scar bog	N/A	9	1.2	13.0	130.6	143.6	0.1	1.1	1.2	4.4	0.0	11.7	11.7	0.0	0.1	0.1
All soils			673	91.7	4.7	37.3	42.0	3.2	25.1	28.2	100	30.9	-9.2	21.8	20.8	-6.2	14.7
Other	Rock, water, lake	N/A	61	8.3	0.0	0.0	0.0					0.0	0.0	0.0			
Total area			733	100	4.3	34.2	38.5					28.4	-8.4	20.0			

(A) SURFACE LAYERS



(B) DEEP LAYERS



(C) TOTAL PROFILE

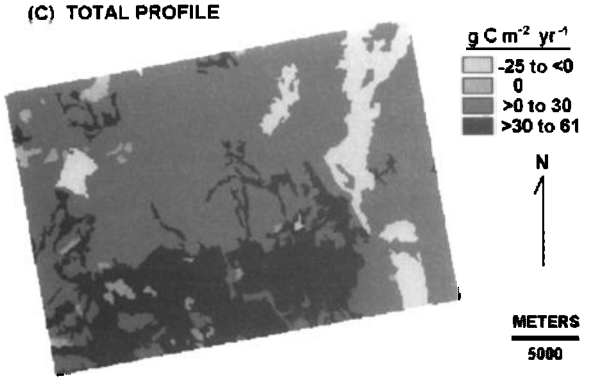


Figure 5. Rates of soil carbon accumulation or loss in the 733 km^2 study area. The maps represent area-weighted averages of (a) surface layers, including moss, (b) deep layers, and (c) total profile. See text for discussion of surface and deep layers.

4. Discussion

The model estimates that average net soil C storage was about 20 g C m^{-2} yr^{-1} over the 733 km^2 study area of northern boreal forest in 1994 (Table 3), which is a modest sink of atmospheric CO$_2$ Using an eddy covariance method, *Goulden et al.* [1998] estimated that the 120 year old Old Black Spruce (OBS) study site had net ecosystem productivity (NEP) ranging from a loss of 70 g C m^{-2} yr^{-1} to a gain of 10 g m^{-2} yr^{-1}. Woody biomass was accumulating 20-40 g C m^{-2} yr^{-1}, thus indicating that the moss and soils were losing 10-100 g C m^{-2} yr^{-1}. The average forest stand age across the 733 km^2 area, however, is 45-65 years, and our analysis shows that stand age is an important factor in soil C accumulation rates, especially for surface soils and moss layers in upland sites. Stands like the 120 year old OBS tower site occupy <10% of the NSA map area. Scaling fluxes measured by eddy-covariation techniques at a few towers (compare Figure 1b, Plates 1a and 1b) in this mosaic landscape of drainage class and stand age, could be misleading. Even so, our estimate of 20 g C m^{-2} yr^{-1} sequestered by soils is modest and is within the range of error and interannual variation reported by *Goulden et al.* [1998].

While studies on interannual variability of C fluxes in boreal forests have concentrated on extrapolating stand-level responses of photosynthesis and respiration to differences in climatic conditions [e.g. *Frolking et al.*, 1996; *Frolking,* 1997; *Goulden et al.*, 1998], our results show that significant interannual variability in regional C exchange rates may also result from interannual differences in the occurrence of fire. For example, the 1981 fire burned approximately 17% of the study area (128 of 733 km^2). The average soil C accumulation rate in 1981 is estimated by our model to have been 27 g m^{-2}. Assuming that burning of the moss layer in this 128 km^2 fire released 2000 g C m^{-2}, then the net soil C flux in 1981 was a net loss of 317 g C m^{-2} yr^{-1} (27 g C m^{-2} yr^{-1} × 0.83 - 2000 g C m^{-2} yr^{-1} × 0.17). For comparison, *Frolking* [1997] estimated that interannual differences in C storage at the OBS tower site varied between 0 and 125 g C m^{-2} yr^{-1} because of physiological response to interannual anomalies in weather. Hence, averaged over large regions, interannual variability in C exchange may result from changes in the lateral extent of fire as much or more than direct responses of the vegetation to climatic conditions.

Putting the importance of fire another way, the release of C from the moss layer by a fire covering only 1% of the area in any year would offset the amount of C stored in soils of the rest of the area (20 g C m^{-2} yr^{-1} × 0.99 ≅ 2000 g C m^{-2} yr^{-1} × 0.01). The fire return interval for Alaskan boreal forests has been estimated to be 150 years [*Kasischke et al.*, 1995], with a range in various North American boreal forest types of 70-500 years [*Payette,* 1993]. If the fire cycle were about 100 years, then our carbon budget for a year with no fire might suggest that the soil C stock may be roughly at steady state over large areas and long timescales. Over millennial timescales, soil C storage rates since the drying of Glacial Lake Agassiz are of the order of only a few g C m^{-2}yr^{-1} [*Trumbore and Harden,* 1997; *Harden et al*, 1997]. However, the incidence of fire is variable over space and time and could be changing in response to climate change and management practices. For an annual C budget of a local site, the time since the last fire is critical. For decadal or centennial scale budgets over the region, fire frequency and its variability over the landscape are clearly important.

A major uncertainty in determining the present and future role of soils as C sources or sinks is the role of the deep organic matter in the C budget of upland soils. Decomposition rates of deep organic layers are an order of magnitude slower than those in surface layers (Table 1), which might lead to the assumption that the deep soil is not important in C cycling. However, large

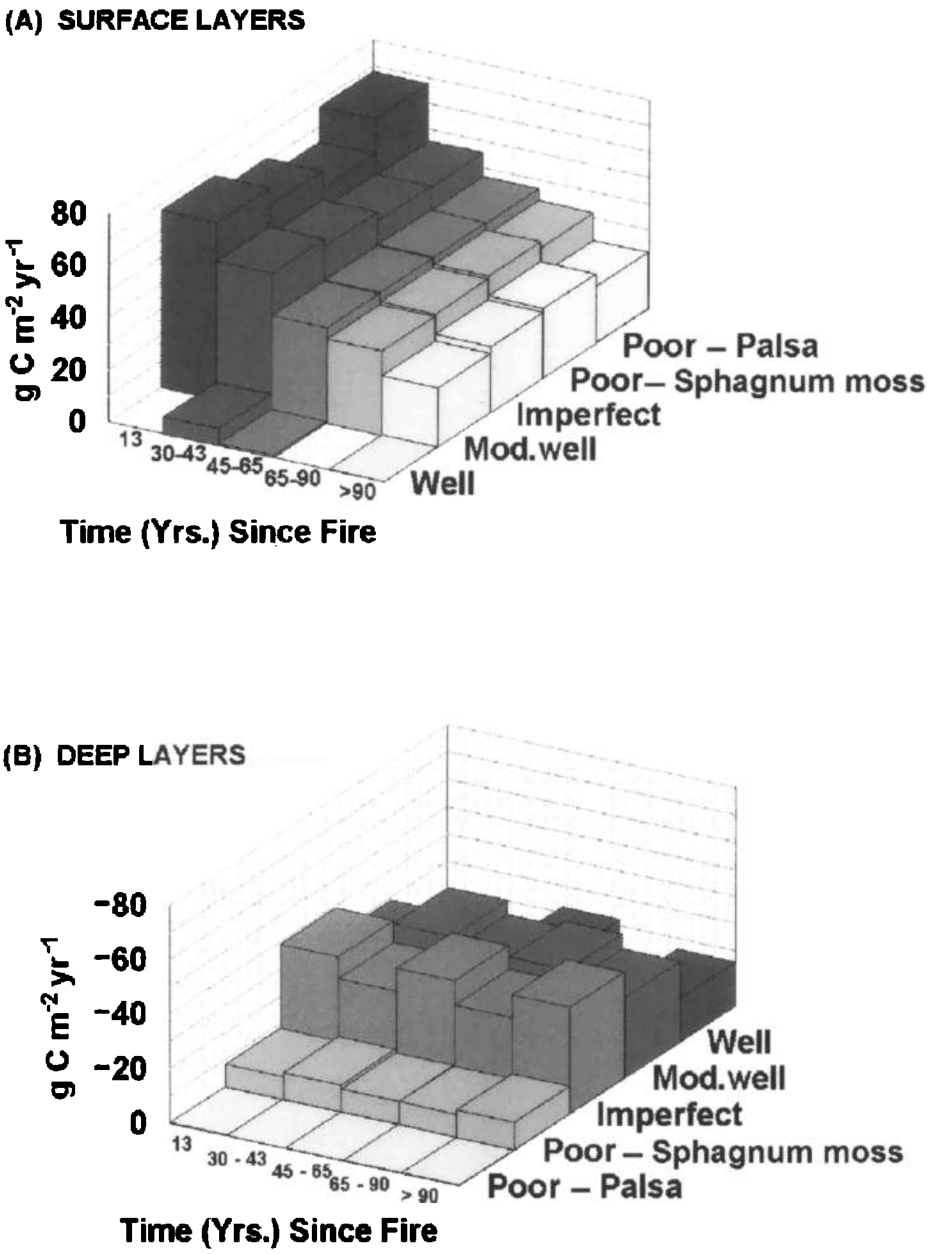


Figure 6. (a) Rates of C accumulation (positive values) in surface layers (including moss) for drainage class and by time since fire (stand age). (b) Rates of C loss (negative values) from deep organic layers (below moss) and mineral soil as a function of soil drainage and time since fire. Fens and collapse scar bogs (not shown) are gaining an estimated 29 and 12 g C m^{-2} yr^{-1}, respectively, in the deep layers.

stores of C are present in the deep layers, so even at slow rates of decomposition, losses on an annual basis are significant, and interannual differences in decomposition of deep soil C can affect the C balance of a whole forest stand [*Goulden et al.*, 1998]. We have assumed that the deep soil C pools show net losses of C in between fire events. Comparison of soil C balance with eddy covariance measurements of NEP [*Harden et al.*, 1997], evidence of increases in late summer soil respiration [*Goulden et al.*, 1998], and radiocarbon measurements in soil CO_2 [*Winston et al.*, 1997] all support this hypothesis

Considerable uncertainties remain about the origin and dynamics of this important deep soil C pool. The radiocarbon data used by *Trumbore and Harden* [1997] to calculate inputs and decomposition constants may have been influenced more by the frequency and severity of burning than by actual decomposition rates of the humic materials. Incubation measurements [*Fries et al.*, 1997; *Moore and Knowles*, 1990] show that deep organic C decomposes rapidly if warmed and dried. These findings suggest that the slow decomposition rates we inferred from radiocarbon studies are constrained by physical

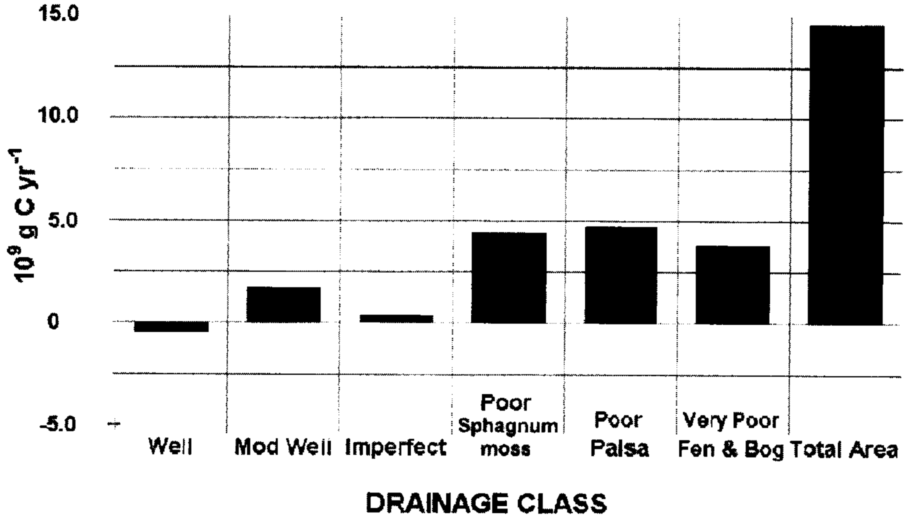


Figure 7. Total annual C soil accumulation (>0) or loss (<0) by drainage class for entire 733 km^2 study area.

conditions (cold and wet) within the soil, rather than by the ability of the organic matter itself to decompose. We cannot, therefore, necessarily predict decomposition rates for this pool should climate change. Although deep soil C has accumulated slowly over millennia, the dynamics of this large C pool may dominate the response of northern boreal forest to future changes in fire frequency or climate.

5. Conclusion

Variation in soil C stocks across the landscape mainly reflects the amount of deep C present as slowly decomposing humic and mineral organic matter and is clearly related to soil drainage. Variation in rates of soil C accumulation and loss is because of both drainage and forest stand age. We calculate net soil C storage averaging about 20 g C m^{-2} yr^{-1} in 1994, a year when none of the area was affected by fire. Significant interannual variability in C storage is expected due to the irregular occurrence of fire in space and time. The future C balance for the region may depend largely on how fire frequency is affected by changing climate and management.

The turnover of deep soil C in these ecosystems deserves more attention, because of the large C stocks present in deep layers, uncertainties in the estimated decomposition constants,

Table 4. Sensitivity Analysis of the Effects of Deep Soil C Decomposition Constants on Simulated Rates of C Accumulation and Loss

	Scenario Decomposition Constants, yr^{-1}		
Drainage Class/Vegetation Type	Reference	Low	High
Well-drained sand/Jack pine	0.01	0.007	0.012
Moderately well-drained clay/Black spruce-feather moss	0.003	0.0006	0.006
Imperfectly drained clay/Black spruce-mixed mosses	0.002	0.0006	0.003
Poorly drained/Black spruce-sphagnum moss	0.0007	0.0005	0.0009
Very poorly drained/Fen and collapse scar bog	0.0004	0.0002	0.0005
	Mean Area-Weighted C Accumulation or Loss[a], g C m^{-2} yr^{-1}		
Soil Horizon	Reference	Low	High
Surface	30.9	30.9	30.9
Deep	- 9.1	+ 4.9	- 21.5
Total profile	21.8	35.8	9.4

[a] Values cover 673 km^2, total area mapped as soils (Table 3).

Table 5. Sensitivity Analysis of C Accumulation in Moss and Surface Soil Layers, Assuming Entire Area (Except Fens and Collapse Scar Bogs) Burned 13, 30, 60, or 120 Years Ago

	Mean Area-Weighted C Accumulation or Loss[a], g C m^{-2} yr^{-1}		
Time Since Fire, years	Surface Layers	Deep Layers	Total Profile
Reference case (1994)	30.9	- 9.1	21.8
13	46.4	- 9.1	37.3
30	37.9	- 9.1	28.8
60	26.8	- 9.1	17.7
120	13.9	- 9.1	4.8

[a] Values cover 673 km^2, total area mapped as soils (Table 3).

and the possibility that decomposition rates in the deep soil could increase as soils warm and become drier. The effects of expected warming and altered drainage patterns on the fate of the immense stores of C in the deep soil of boreal forests must be understood to determine how climate change will affect the global carbon budget.

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