

Soil Carbon Stocks and Soil Carbon Quality in the Upland Portion of a Boreal Landscape, James Bay, Quebec

David Paré,^{1*} Jessica L. Banville,^{2,3} Michelle Garneau,^{2,3}
and Yves Bergeron⁴

¹Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, Quebec, Quebec G1V 4C7, Canada; ²Département de Géographie, Université du Québec à Montréal, Montreal, Quebec H3C 3P8, Canada; ³GEOTOP UQAM-McGill, Université du Québec à Montréal, Montreal, Quebec H3C 3P8, Canada; ⁴Chaire Industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 Boulevard de l'Université, Rouyn-Noranda, Quebec J9X 5E4, Canada

ABSTRACT

As part of a multidisciplinary project on carbon (C) dynamics of the ecosystems characterizing the Eastmain Region Watershed (James Bay, Quebec), the objective of this study is to compare the soil C stocks and soil organic matter quality among the main upland vegetation types in a boreal region subjected to a high fire frequency. On average, the organic layer contained twice the amount of C than the mineral soil. Closed canopy vegetation types had greater C stocks both in the mineral and in the organic layers than the other more open canopy vegetation types. Landscape features such as drainage and surficial deposit could not discriminate between vegetation types although closed vegetation types were on average found on wetter site conditions. Average soil C contents varied more than 2-fold across vegetation types. On the opposite, except for the organic layer C:N ratio, which was smaller in closed vegetation

types, other measured soil organic matter properties (namely specific rate of evolved C after a long-term incubation, hydrolysis acid-resistant C as well as the rate of changes in soil heterotrophic respiration with increasing temperature (Q_{10})) remained within a narrow range between vegetation types. Therefore, total soil C stocks were a major determinant of both labile C and estimated summer soil heterotrophic respiration rate. The homogeneity of soil organic matter quality across the vegetation types could be attributable to the positive relationship between soil C storage and soil C fluxes observed in this landscape experiencing a high fire frequency. The low variability in soil C quality could help simplify the modelling of soil C fluxes in this environment.

Key words: soil C cycling; boreal forest; soil organic matter quality; scaling; landscape; fire cycle.

Received 12 October 2010; accepted 6 February 2011;
published online 26 March 2011

Author Contributions: Paré took the principal role in writing and analyzing the data. Banville coordinated and conducted field and laboratory analysis and contributed to data analysis and writing. Garneau coordinated the overall project. Bergeron assisted in the analysis and interpretation of the influence of landscape features and fire dynamics.

*Corresponding author; e-mail: dpare@nrcan.gc.ca

INTRODUCTION

Boreal forests and their associated peatlands are considered as the largest terrestrial carbon (C) reservoir on the planet (IPCC 2001), mostly because of their important surface area (approximately 14×10^6 km²) and their large soil C densities.

Canadian boreal forests have been considered as a large net C sink since the last deglaciation. However, recent studies suggest that terrestrial C sinks are weakening (Canadell and others 2007), and current changes in disturbance regimes (Le Goff and others 2008) could significantly affect this equilibrium by allowing boreal forests to shift from a sink to a small net source of C (Kurz and Apps 1999; Kurz and others 2008). Moreover, this biome is among those expected to experience some of the greatest climate change over the next century (Bhatti and others 2003), which could lead to a significant impact on the global C cycle (Kurz and others 2002) because of a potential increase in soil respiration and enhanced forest fire activity (Flannigan and others 1998). These changes could lead to a positive feedback in the global C sequestration potential (Cox and others 2000; Knorr and others 2005). Nevertheless, the maintenance of soil C reservoirs given the possibility of a warmer climate is still a matter of debate (Kirschbaum 2006) with some studies predicting greater net C losses (Bellamy and others 2005), whereas others predicted increased C storage (Liski and others 1999).

The dynamics of soil organic matter are generally depicted by pools with different turnover rates. The representation of soil organic matter dynamics with a unique decomposition rate or a single C pool generates incorrect estimates, mostly an underestimation of the short-term response and an overestimation of the long-term response of change in C input and output (Trumbore 2000). The most active pools represent a small proportion of the total soil C stock but are responsible for most of the C fluxes (Paul and others 2001). These labile pools are clearly reactive to temperature changes and responsible for most of the changes in soil C in relation to climate change (Melillo and others 2002; Davidson and Janssens 2006). Decomposition of recalcitrant organic matter is also very sensitive to temperature but because of its very small contribution to soil respiration and the lack of knowledge concerning the relationship between temperature changes and carbon stabilization processes, it is believed that losses from these reservoirs would occur very slowly (Davidson and Janssens 2006).

Accumulation of organic C in soils and the proportion of C allotted to soil C pools with different turnover rates tend to vary with vegetation type (Gower and others 2001; Bhatti and others 2002; Yu and others 2002), but this has rarely been quantified by empirical methods. These variations are linked to different factors, including litter quality variations with forest composition (Paul

and others 2002), climate (Trumbore and others 1996), soil texture and types of minerals (Torn and others 1997; Côté and others 2000), drainage and topography (Parton and others 1987). Moreover, apart from modelling approaches, only a few studies have investigated the variability in soil organic C content and quality among the different vegetation types covering a boreal landscape at the ecodistrict level (for example, Borken and others 2002; Ladegaard-Pedersen and others 2005). Labile soil organic matter is loosely defined and estimates of its importance may vary considerably due to the lack of a standardized methodology (long-term incubation, acid hydrolysis, light and heavy fractions, and so on) (Paul and others 2006). Nevertheless, McLaughlan and Hobbie (2004) stipulated that these methods are relatively well correlated among themselves and, in the present experiment, long-term incubation was chosen to determine the active C pool as in other studies (Dalias and others 2001; Paré and others 2006; Rey and Jarvis 2006).

This study is part of a multidisciplinary project that aims to determine the C budget (CO_2 and CH_4) from natural boreal ecosystems before and after impoundment of a hydroelectric reservoir (Eastmain-1). As part of this project, the main objective of this study is to determine whether the five main vegetation types classified with remote sensing from Spot imaging (Grenier and others 2008) represent homogeneous units in terms of soil C stocks, soil C lability, and reactivity to temperature change. These characteristics of soil organic matter were also used to estimate field rates of heterotrophic soil respiration during the summer period.

METHODS

Study Area and Sites Description

The study was conducted in the Eastmain River Watershed in the James Bay Lowland (Figure 1), northern Quebec ($51^\circ 56' - 52^\circ 20' \text{ N}$, $75^\circ 05' - 76^\circ 10' \text{ W}$), at the northern limit of the *Picea mariana*-feathermoss bioclimatic region (Robitaille and Saucier 1998). The study area covers nearly 2,500 km², and 24% of this territory is now occupied by a hydroelectric reservoir of 603 km² created in 2005 (Figure 1). Annual average temperature is -2.4°C and precipitation reaches 700 mm per year (Wilson 1971). The region is punctuated by numerous lakes and undulating hills (max. 175 m ASL) from Precambrian bedrock and surficial deposits originating from the last Wisconsinian glaciation. These quaternary deposits are mainly from

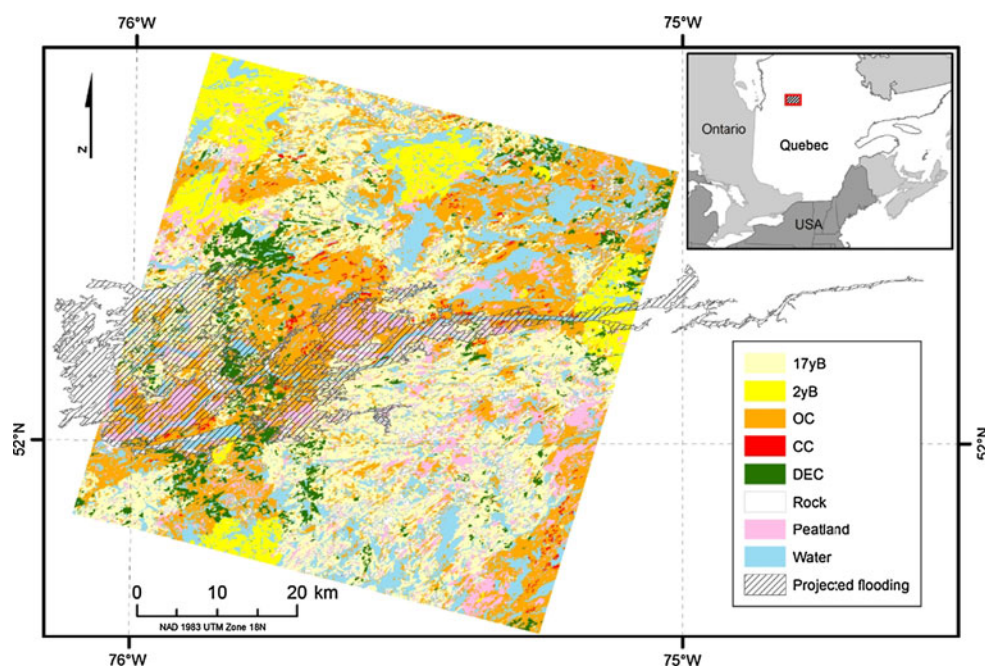


Figure 1. Map of the vegetation types identified with Spot images as well as localization of the projected flooded area on the Eastmain River Watershed, James Bay, Quebec, Canada.

glacial, lacustrine, and alluvial origins and are characterized by their coarse texture and thinness. Soils are classified as Regosol, Organic, Humo-ferric, and Ferro-humic Podzol (CSSC 1998). A thick organic layer has developed because of the soil's acidic conditions ($\text{pH} < 5$) and the cold and humid climate. Soil texture varies from fine silt to silty sand and drainage from well drained to poorly drained. Regional vegetation belongs to the *Picea mariana*-feathermoss domain mostly dominated by coniferous species with a forest floor covered by bryophytes and lichens. Fire is the main disturbance that drives the vegetation dynamics in the region. Open vegetation due to poor post-fire forest regeneration is also common in this area (Payette and others 2000).

We used the regional vegetation classification and mapping of Grenier and others (2008), which was developed for the study area using Spot imagery and field surveys. Five major vegetation types were considered for our study given their extent: (i) coniferous-closed canopy (CC), (ii) coniferous-open canopy (OC), (iii) deciduous (DEC), (iv) 2-year-old burned forest (2yB), and (v) 17-year-old burned forest (17yB). The second type, open canopy coniferous forest (OC), is common at this latitude due to frequent forest regeneration failure caused by complex climate–fire–insect interactions (Payette and others 2000). As shown in Table 1, open vegetation types, both from recent fire origin (2–17 years) or older, make up the great majority of the upland landscape (>90%). According to ecological classification maps from Leboeuf and others

(2009), till deposit with mesic drainage conditions make up a very large proportion of the landscape for any vegetation type (Table 1). Soils are of a coarse texture and the sand fraction dominates (>50% sand). The forest floor in CC is dominated by *Pleurozium schreberi* and some *Sphagnum* spp. patches, whereas lichens such as *Cladina* spp. are dominant in OC, where deposits are mostly sandy with a rapid water evacuation. Open and closed canopy coniferous forests (OC, CC) are dominated by black spruce (*Picea mariana* Mill. BSP.) and jack pine (*Pinus banksiana* Lamb.). Deciduous stands (DEC) are predominantly composed of trembling aspen (*Populus tremuloides* Michx.), whereas white birch (*Betula papyrifera* Marsh.) has only been found sporadically. Peatlands (mostly open peatbogs and few forested peatlands) were not integrated in this study mostly because these ecosystems do not present the same carbon processes and dynamics and have been extensively studied by other scientists involved in the project (Van Bellen and others, in press).

Soil Sampling and Preparation

Soils were sampled in July 2007 from nine distinct stands for each of the five vegetation types studied. A single 100 m² plot was selected within each studied stand for soil sampling and vegetation description. Five of the nine stands per vegetation type were randomly retained for laboratory incubation at 29°C and only one reference stand (no. 1)

Table 1. Breakdown of the Area Covered by the Different Vegetation Types Classified and Mapped using SPOT Imagery into Different Surficial Deposit and Drainage Classes as Determined by Ecological Landscape Classification and Mapping for the Whole Study Area as well as Average Drainage Classification for the 9 Stands Sampled per Vegetation Types

Upland Vegetation types ¹	% Area by veg. type ²				% Of total upland area ³			Avg. drainage ⁴ (field estimate)	
	Deposit				Drainage type				
	Glacial	Fluvio- glacial	Organic	R < 25 cm	Xeric	Mesic	Hydric		
17yb	81	7	8	1	8	80	8	40	1.6
2yb	75	13	7	3	13	73	7	11	1.6
OC	74	12	11	1	9	75	11	40	1.9
CC	89	6	2	2	5	89	2	1	2.7
DEC	89	4	1	3	7	87	1	8	3.3
Overall	85	8	6	2	1	87	12		

% of area excluding water bodies, peatlands and non-vegetated areas, and average drainage class for the nine sites investigated per type from a field assessment (classes 0–6, 6 being the wettest).

¹From Grenier and others (2008).

²From Leboeuf and others (2009).

³Excluding peatland and non-vegetated areas.

⁴Averages from a classification based on a scale of 0 to 6 (values ranged from 2 to 5).

per vegetation type was retained for soil temperature and litterfall measurements as well as for incubation at multiple temperatures.

One soil pit was dug in each plot to determine soil depth and drainage. Drainage was classified into seven categories (from 0 to 6) ranked in order of increasing wetness. Most plots fell within drainage classes 2 and 3, and all plots were within classes 2 and 5. At the four corners of each plot, the organic layer (FH), equivalent to the Oi and Oe/Oa layers, was collected with a 10 cm × 10 cm template and the mineral soil was sampled with a 5-cm diameter metal pipe at a depth of 20 cm. It was not possible to sample at a greater depth because of the abundance of large pebbles and boulders and because of soil thinness. Nevertheless, soil depth assessments indicated that only the closed forest type had an average mineral soil depth exceeding 20 cm, with mean depths of 22 ± 7 and 25 ± 5 cm for CC and DEC, respectively, whereas it was 16 ± 3.5, 14 ± 3.5, and 19 ± 2.5 cm deep in 2YB, 17YB, and OC, respectively. Once sampled, soils were maintained at 4°C in a cooler until processing in the laboratory. Coarse fragments (woody debris, roots and rocks) were removed by hand to preserve soil structure and samples were pooled per plot and soil layer for subsequent analysis. The samples of five stands per vegetation type were retained for laboratory incubation. Organic and mineral soil samples were gently sieved at 6 and 4 mm, respectively, for the incubation experiment (Paré and others 2006; Rey and Jarvis 2006). Sub-samples were further air-dried and sieved at 2 mm

for other conventional physical and chemical analyses, whereas they were finely ground for CN, CEC and Fe-Al determinations.

Soil temperature used for modelling heterotrophic respiration was measured every hour in each reference stand for the period from June 6 to October 4 with two data loggers (Thermocron® and iButtons® ds191Z-F5) buried at 10 cm in the mineral soil. Mean daily temperatures at each site were used for the computation. Aboveground litterfall was collected twice in 12 wood litter traps of 0.7 m² at each reference stand over a period of 1 year (g m⁻² y⁻¹).

A drainage class was assigned in the field for each plot. As with the ecological land classification (Leboeuf and others 2009), field drainage class determination revealed that although the closed forest types (CC and DEC) are found on a wide range of drainage conditions, they are found on average in slightly wetter conditions than the open forest types (Table 1). We considered the estimates of drainage conditions in the studied plots determined from field observations to be more accurate than those given by the ecological land classification.

Laboratory Analysis

Samples were analyzed for their carbon and nitrogen contents using a Leco CNS 2000 (Leco Corporation, St. Joseph, Michigan, USA). Non-hydrolyzable C content was determined by the acid hydrolysis technique using 6 M HCl to reflux the material at

116°C for 16 h (McLaughlan and Hobbie 2004). Cation exchange capacity (CEC) was determined by summing up exchangeable cations (Carter 1993) extracted with 0.1 M BaCl₂, which were analyzed by atomic absorption spectrophotometry. pH was determined both in water and in 0.5 M CaCl₂ using a PHM82 pH meter (Radiometer Copenhagen) (Carter 1993). Soil texture was determined by humid sieving (Hoey 2004) coupled to a laser diffraction using a sedigraph (Analysette 22, Fritsch Laborgeräte), whereas bulk density was measured after drying at 105°C.

Incubation

The incubation experiment is time-consuming and only five randomly selected stands per vegetation types could be analyzed. The methodology that was used is described in greater detail in Paré and others (2006). Seventy microcosms were prepared: 50 microcosms were incubated at 29°C (5 vegetation types × 5 stands × 2 soil layers) and 20 additional microcosms from the five reference sites only were incubated at two additional temperatures (2 and 14°C) (5 sites × 2 layers × 2 temperatures). Fifty grams of dry weight equivalent of mineral soil and 8 g of organic material at 100% WHC were placed into 100 ml plastic containers filled with glass wool at the bottom. These containers were perforated to facilitate evacuation during leaching with K₂SO₄ 0.005 M and humidification. These manipulations made it possible to maintain soil humidity and remove residuals from decomposition during the incubation period. Microcosms were placed into glass jars and incubated in growth chambers at a constant humidity level for 164 days. Samples were submitted to high temperatures to obtain in an adequate delay the proportion of readily mineralizable C (Dalias and others 2001; Rey and Jarvis 2006). Jars were kept open to maintain aerobic conditions except during CO₂ measurements, when they were hermetically closed to let CO₂ accumulate. Moisture contents in the samples incubated at 29°C were monitored by weighing the entire microcosm and by adding deionized water (Milli-Q) to the soil. This humidification operation, as well as leaching, was conducted twice a month for the duration of the experiment.

Carbon Mineralization Measurements

Carbon mineralization was measured every week for the first month and then once a month until the end of the experiment. Nine periods of measurements were conducted during which the rate of

mineralization was calculated as the CO₂ efflux emitted over 24 h. For each microcosm, 10 ml were collected with a needle and a syringe from the closed jar through a septum made in the lid and gas concentrations were measured with a Li-COR LI-6200 (LI-COR® Application Note #121). Evolved CO₂ from each microcosm was calculated according to Paré and others (2006) and the mineralized C (C_m) expressed as mg (C) per g of initial soil C was calculated using the following equation:

$$C_m = C_{m-1} + (R_p + R_{p-1})/2 * (D - D_{-1})$$

where C_m is mineralized C (mg C-CO₂ g⁻¹ C_{org}), R is the daily respiration rate (mg C-CO₂ g⁻¹ C_{org} d⁻¹), p is the incubation period (1–9), and D is the day when the incubation started. The C mineralization rates are expressed as µg CO₂ g⁻¹ C_{org} h⁻¹.

Data Analysis

The cumulative curves of mineralized C were fitted to a first-order kinetic model proposed by Stanford and Smith (1972). This model is used to estimate the labile fraction of C and the rate at which it is mineralized. This model estimates a unique pool of labile C in which the mineralization rate depends on the temperature. Cumulative mineralized C at the three incubation temperatures was calculated separately for organic and mineral layers and fitted to the following model:

$$C(t) = C_0(1 - e^{-kt})$$

where C(t) is the cumulative C mineralized at time t (mg C g⁻¹ initial C), C₀ is the labile fraction, and thus the potential mineralizable C (mg C g⁻¹ C_{org}), k(d⁻¹) is the constant release rate for the mineralization of C, and t is time. We used values for the full incubation period (164 days) for the analysis. For the reference stands only, mineralization curves from the three temperatures of incubation were used to estimate a Q10 value expressing the change in the rate of mineralization (k) with temperature change as follows:

$$k = k_{\text{ref}}((Q10_k)^{(T-T_{\text{ref}})/10})$$

The experimental data were fitted to the model using the non-linear mixed procedures in SAS (proc non-linear mixed, SAS Institute Inc., Cary, NC). Because C₀ and k are both influenced by temperature and organic matter properties and are often correlated, the product of C₀ * k represents a better estimate of labile C than these parameters used independently.

Statistical Analysis

Differences between vegetation types were analyzed by one-way ANOVAs, and the Tukey–Kramer test was used to detect significant differences between each pair of variables. C stocks and mineralized C were log-transformed to meet the assumptions of normality and homogeneity of variance. All statistical analyses were performed using JMP version 7.0.1 (SAS Institute Inc., Cary, NC).

Estimation of Soil Heterotrophic Respiration

Soil heterotrophic respiration rates were estimated for each of the five stands per vegetation types for which soil C incubations were conducted for the June 8 to October 4 period during which soil temperature information was available. Briefly, the labile C pool and its rate of mineralization at 29°C were derived from total soil C pool estimates and from the equation-derived parameters for each stand, whereas changes in the rate of C mineralization of the labile pool with changes in

temperature (*Q10*) as well as the soil temperature data came from the reference stands only. We assumed steady state conditions: soil heterotrophic respiration comes from the labile pool only and the continuous production of litter and exudates replaces the evolved labile C on a daily basis such that C_o (that is, remaining labile C) remained constant.

RESULTS

Soil Organic Carbon Stocks

A higher C content was observed in closed vegetation types (CC and DEC) when compared with open vegetation types (17YB, 2YB, OC) both in the organic layer and the mineral soil and in the total of both layers (Figure 2A, C, E). The C content of the organic layer was more than twice as important as that of the mineral soil with average values of 6.36 kg C m⁻² compared with 2.92 kg C m⁻², respectively. Average vegetation type soil organic C contents from combined forest floor and 0–20 cm mineral soil ranged from 6.2 to 13.3 kg C m⁻² (Figure 2E, F). The forest floor of closed vegetation types (CC and DEC) showed a consistent trend for

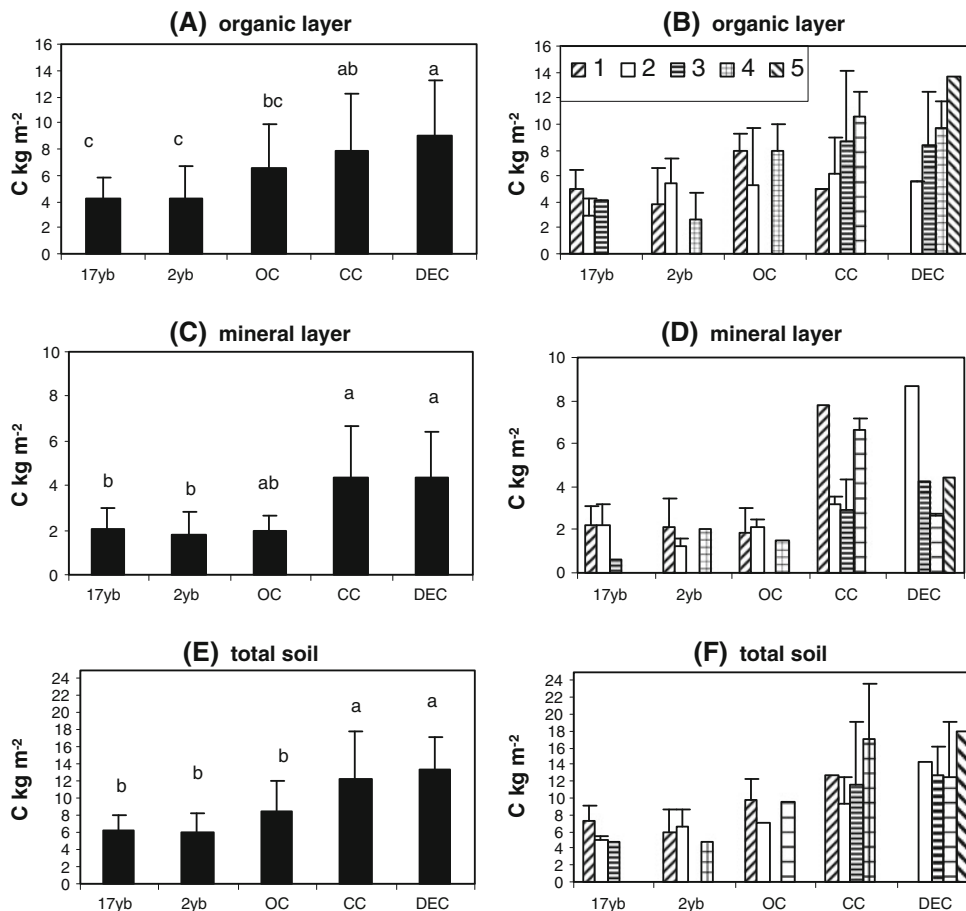


Figure 2. Total mean soil organic C (kg C m⁻²) in the organic layer, the mineral soil layer (0–20 cm), and in both layers combined for each vegetation type (A, C, E, respectively) and for each vegetation type further divided into drainage classes (1–5; 1 being the driest). Error bars represent the standard deviation from the mean. The black bar represents the mean of the nine sampled plots. Bars labelled with different letters differ significantly (One-way ANOVAs: $P > 0.005$). **A** Organic layer ($P = 0.0153$); **C** mineral layer ($P = 0.003$); **E** sum of the two layers ($P = 0.0001$).

increased C stocks with slower drainage classes (Figure 2B). This trend was not observed for other vegetation types or for the mineral soil, but the number of repetitions in some drainage classes/vegetation composition types was low. Closed vegetation types were found on a wide range of drainage conditions but on average they were found in wetter site conditions than open vegetation types (Table 1). Within a similar drainage class, closed forest types generally showed a greater C content compared with open vegetation types as can be seen in Figure 2. Unfortunately, these differences could not be tested statistically because of the lack of some vegetation type-soil drainage combinations. An analysis of covariance with drainage as a covariable was not possible because the relationship between drainage and OM content was not consistent across vegetation types.

Soil Organic Matter Properties

Labile C can be estimated by deriving daily cumulative specific mineralization rates ($C_o * k$) from

non-linear equations or simply by considering cumulative-specific C mineralized at the highest temperature of incubation (Paré and others 2006). For both soil layers, cumulative-specific C mineralized at the highest incubation temperature (29°C) (Table 2; Figure 3) showed little variability across vegetation types and differences were not significant between vegetation types for both the organic layer and the mineral soil. In the forest floor, values ranged from 77 ± 12 to 99 ± 28 mg C g C_{org} total⁻¹, and in mineral soil they ranged from 50 ± 25 to 63 ± 19 mg C g C_{org} total⁻¹, indicating that the proportion of cumulative evolved C was more important in the organic layer than in the mineral soil. The results of the first-order kinetic model of the reference stands are presented in Table 2. The product of $C_o * k$, expressed as evolved C per initial C weight per day (mg C g⁻¹ C_{org} day⁻¹), illustrates the portion of total C that is mineralized on a daily basis because C_o is the fraction of labile C and k is the daily rate of mineralization of this fraction. Because these two parameters are inversely correlated, it can be misleading to interpret them

Table 2. Soil Organic Matter Properties

Parameter	17yB	2yB	OC	CC	DEC	P	F	d.f. error and nb of replicated stands
<i>Organic</i>								
$C_{min(29^\circ C)}$ (mg C g ⁻¹ C_{tot})	91 ± 13	81 ± 25	92 ± 27	77 ± 12	99 ± 28	0.498	0.873	19-5
$C_{min(29^\circ C)}$ (g C m ⁻²)	368 ± 81	272 ± 164	347 ± 164	519 ± 313	638 ± 268	0.152	1.897	19-5
$k_{(29^\circ C)}$ (d ⁻¹ * 1000)	0.72 ± 2.48 b	1.01 ± 1.04 b	2.64 ± 2.77 b	2.41 ± 3.83 ab	4.21 ± 3.2 8 a	0.004	5.504	19-5
$C_o * k_{(29^\circ C)}$	0.50 ± 0.09 c	0.47 ± 0.12 c	0.65 ± 0.22 ab	0.54 ± 0.15 bc	0.74 ± 0.24 a	0.020	3.768	19-5
Q10	2.6	2.6	3.1	2.3	2.3	–	–	–
Acid insoluble %C	82 ± 3	78 ± 5	78 ± 6	80 ± 8	76 ± 7	0.3897	1.059	38-8
C:N	44 ± 4 b	50 ± 7 a	50 ± 8 a	37 ± 5 c	24 ± 3 d	0.0001	49.03	40-9
<i>Mineral</i>								
$C_{min(29^\circ C)}$ (mg C g ⁻¹ C_{tot})	54 ± 18	63 ± 19	55 ± 10	50 ± 25	55 ± 18	0.9684	0.151	19-5
$C_{min(29^\circ C)}$ (mg C m ⁻²)	102 ± 37 c	127 ± 38 bc	114 ± 15 bc	210 ± 56 ab	236 ± 101 a	0.002	6.223	19-5
$k_{(29^\circ C)}$ (d ⁻¹ * 1000)	0.0024	0.0018	0.004	0.0033	0.0034	0.681	0.579	19-5
$C_o * k_{(29^\circ C)}$	0.38 ± 0.21	0.44 ± 0.14	0.45 ± 0.09	0.45 ± 0.36	0.47 ± 0.24	0.896	0.2664	19-5
Q10	2.1	2.6	2.2	2.2	2.8	–	–	–
C:N	22 ± 8	21 ± 7	26 ± 8	25 ± 4	21 ± 4	0.4454	0.9499	40-9

Values are averages and standard deviation of the five or nine replicated sites per vegetation type, except Q10, which is estimated for the reference stands only. C_{min} is the cumulative amount of evolved CO₂ during the full incubation (164 days). C_o is the estimated labile fraction of C and $k_{(29^\circ C)}$ is the daily rate of mineralization of this pool at 29°C, whereas Q10 expresses the variation in the rate of mineralization with a change in temperature. $C_o * k$ is estimated for each incubation temperature and represents the specific rate of C respired per day (mg C g⁻¹ C_{org} day⁻¹). Probability, F value and degree of freedom of the model error term together with the number of true replicates are given. The analysis was conducted on log values, but the averages and standard deviations are untransformed values. Bold P values indicate significant differences between vegetation types at the 5% level. Vegetation type averages followed by similar letters are not significantly different at the 5% level.

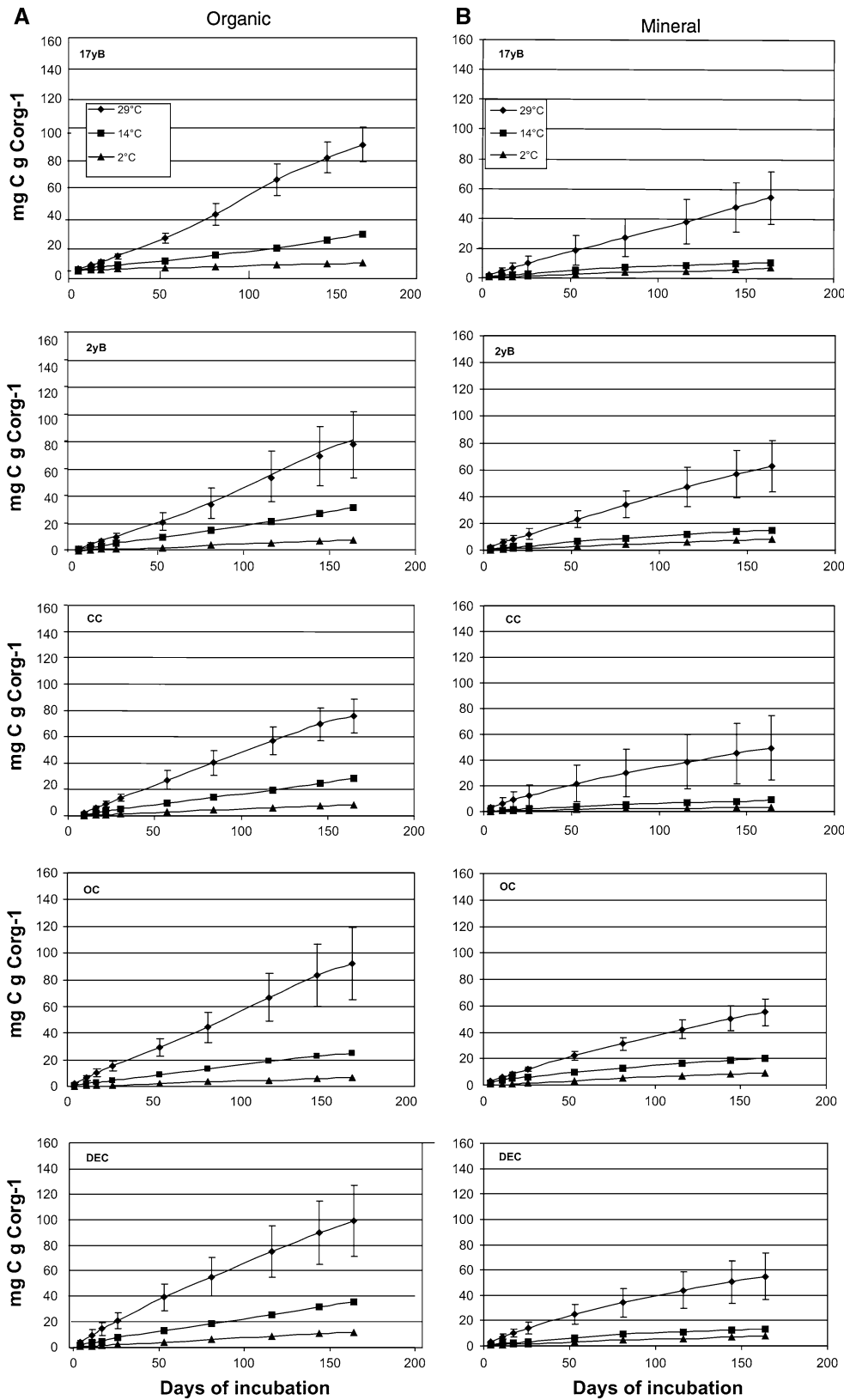


Figure 3. Carbon mineralization rates (mg C g C_{tot} d⁻¹) during the course of a 164-day incubation in **A** the organic layer and **B** the mineral layer, for each forest type. Error bars represent the standard deviation from the mean for the 29°C incubation, whereas values for other incubation temperatures are for the reference stands only.

individually. The daily rate of C mineralization (C_o * k) showed significant differences between vegetation types in the organic layer only, with the

DEC and OC types showing the highest values and the two burned types the lowest, whereas CC was intermediate (Table 2).

The Q_{10} values were determined for the reference stands only. These values ranged from 2.3 to 3.1 for the organic layer and from 2.1 to 2.8 for the mineral soil. A closer look at the data indicates that the amount of cumulative mineralized C varied significantly between 14 and 29°C in all cases ($P < 0.05$), but not between 2 and 14°C ($P > 0.05$). This is in agreement with Rey and Jarvis (2006) who showed that levels of activity of organisms are very low below 10°C.

The proportion of organic layer non-acid hydrolyzable C was very constant, averaging 80% of total organic C, and not significantly different between vegetation types (Table 2). The C:N ratio was one of the only properties showing a clear contrast between open vegetation types and closed forest types as well as between conifers and deciduous species. A much narrower ratio of 24 for deciduous forests and 37 for coniferous forests contrasted with ratios nearing 50 in the open forest types, whereas that of the mineral soil was constant across all vegetation types (Table 2).

When expressed on a surface basis (m^2), the cumulative mineralized C at 29°C was higher in the organic layer than in the mineral soil. For both layers, DEC showed the highest values with 638 and 236 mg C m^{-2} for the organic layer and the mineral soil, respectively, whereas open vegetation types showed the lowest values. CC stands, which had the lowest estimates of specific mineralized C in both soil layers, showed high values when expressed on an areal basis (Table 2).

Seasonal Heterotrophic Respiration

The estimates of soil heterotrophic respiration rates presented in Figure 4 are derived from laboratory-determined C mineralization parameters, field soil C stocks and field soil temperature. Mean soil daily temperature varied from 4.3 to 18.8°C and there were no strong trends in cumulative degree-days with vegetation types (data not presented). Estimated cumulative organic layer heterotrophic respiration rates varied widely across vegetation types. The average value per vegetation type varied by a factor of 6 as it ranged from 338 kg C ha^{-1} in the 2yB stands to 2091 kg C ha^{-1} in the DEC ones. The magnitude of change in the mineral layer was lower (factor of 3), ranging from 184 to 526 kg C ha^{-1} for 2yB and DEC, respectively (Figure 4). The proportion of mineralized C was greater in the organic layer, where it varied from 1.3 to 2%, than in the mineral soil layer, where it varied from 0.5 to 1.4%. In general, the pattern observed across vegetation types was coherent with the estimates of

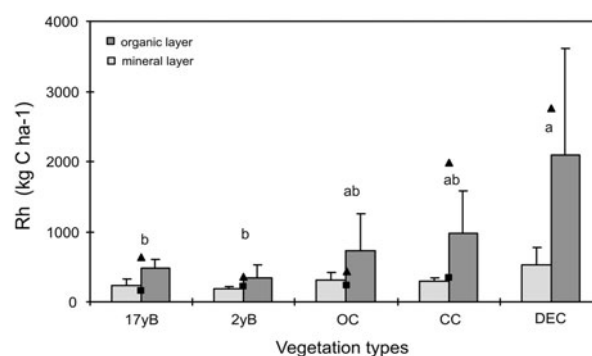


Figure 4. Estimated soil heterotrophic respiration based on soil temperature and components of soil respiration (Table 2) for each vegetation type and soil horizon. Error bars represent the 95% confidence interval and *black triangles* and *squares* correspond to the reference sites' values in the organic and mineral layer, respectively. Soil temperature was measured from June 6 to October 4, 2007 at a 10-cm depth in the mineral soil. Soil temperature as well as Q_{10} were derived for the reference sites only (1 site per vegetation type) and values were used for all five replicated stands, whereas soil C stocks, the proportion of labile C (C_o) as well as the daily rate of mineralization of this pool at 29°C ($k_{(29^\circ\text{C})}$) were derived from the five sites per vegetation type considered for laboratory incubation.

cumulative C mineralization during the laboratory experiment reported on a square meter basis in Table 2.

DISCUSSION

Soil Carbon Stocks, Vegetation Types and Drainage

Total soil C stocks ranged from 6.1 to 13.4 kg C m^{-2} across vegetation types and were within the range of values reported by Bhatti and others (2002), but higher than those estimated by Yu and others (2002) and Gower and others (1997) for comparable vegetation types in western Canada's boreal forest soils. These differences may be due to differences in precipitation regimes between eastern and western boreal regions as the former are under the influence of a humid maritime climate. For all vegetation types, the organic layer stored significantly more C than the mineral soil.

Higher soil C stocks were found in closed vegetation types (DEC and CC). This is somewhat surprising because in boreal regions open forested woodlands are often associated with peatlands with poor drainage conditions and deep accumulated organic sequences (Simard and others 2007) but in this study, peatlands, which represented 14% of

the terrestrial landscape, were not considered. The current fire cycle of the study area is extremely short (<100 years; Mansuy and others 2010), and in eastern Canadian regions experiencing a high fire frequency, the occurrence of open canopy forests has been associated with regeneration failure rather than with site conditions (Jasinski and Payette 2005). Vegetation types could not be linked to specific deposit and drainage conditions determined from the landscape ecological classification map (Leboeuf and others 2009). Determination of drainage conditions during field survey revealed that although all vegetation types can be found on a relatively wide range of drainage conditions, closed canopy types were on average found in wetter site conditions (Table 1). Soil C stocks were also associated with drainage conditions but this relationship was found only for closed vegetation types where more soil C was found in plots showing a slower drainage. Also, within a given drainage class, the total amount of soil C was generally higher in the closed vegetation types than in the open types (Figure 2). These results indicate that both factors, namely, slower drainage conditions as well as the presence of a closed canopy forest, are associated with greater accumulation of C in the soil. Closed vegetation types showed, on average, a deeper soil (22 and 25 cm in CC and DEC, respectively) compared with open vegetation types (16–19 cm), suggesting that soil depth may also contribute to the maintenance of closed stands and to greater soil C stores, especially in the mineral soil. According to Johnstone and others (2010), two main factors are thought to control the depth of the organic layer in boreal forests: (1) the balance between the production and decomposition of plant litter and (2) the amount of soil organic matter that escapes fire combustion. Both factors are potentially playing a role in explaining the higher C stocks of closed stands in this study.

Aboveground litterfall rates, which were measured on one stand per vegetation type over a 1-year period, confirmed, as expected, that C input to the soil through litterfall was much greater in closed than in open forest types (DEC $>$ CC $>$ OC $>$ 17yB $>$ 2yB, respectively; 298 $>$ 277 $>$ 159 $>$ 120 $>$ 26 g m⁻² y⁻¹). Because closed forest stands on average had slower drainage conditions, litter decomposition may also have been slower, with all other conditions, such as litter quality, being equal. Callesen and others (2003) also found that greater soil C stores were associated with higher net primary production on well-drained soils across Scandinavia, and such a relationship would perhaps not have been observed if open forested peatlands would have been included.

Soil moisture conditions may affect fire severity (Harden and others 2000). It is therefore possible that the closed forest types (DEC and CC), because of slower drainage conditions and a thicker organic layer, are less susceptible to severe burning and high C losses, which could contribute to a longer-term C storage in the soil (Manies and others 2001). This suggests that such soil conditions may increase the resilience of closed forests to fire disturbance. Fire severity is also related to vegetation composition, and highly severe fires are more likely to occur in stands where the abundance of conifers is high and that of trembling aspen is low (Epting and Verbyla 2005). Lower fire severity in deciduous stands composed of trembling aspen could therefore help to explain the higher soil C densities found in these stands.

Jasinski and Payette (2005) documented that open forest woodlands are frequently observed at these latitudes and that they often persist for centuries, qualifying them as alternative stable states. In addition, Girard and others (2008) reported a recent (last 50 years) rapid expansion of open lichen woodlands within the closed-crown boreal forest at similar latitudes as this study, with possible influence of severe fires and spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreaks. These observations as well as ours suggest that a given site type may either be occupied by an open or a closed forest and that disturbance history is an important determinant of forest regeneration success or failure. This is in agreement with Johnstone and others (2010) who commented that intermediate positions along moisture gradients, that is, conditions that would apply to most of our study plots, are most vulnerable to fire-initiated loss of resilience.

Greater soil C stocks in closed forest stands may be explained by different factors that are interrelated. These factors and their influence on soil organic matter accumulation are illustrated in Figure 5. Fire history is a major external factor that can override the influence of site characteristics as severe and repeated disturbances over a short interval could limit tree regeneration (Girard and others 2008). Nevertheless, site conditions such as deeper soils and slower drainage may decrease fire severity and increase the resilience of forest regeneration. All these factors may contribute to greater soil C storage as well as promote positive feedback loops on soil organic C through greater rates of C input to the soil through litter production, slower organic matter decomposition rates, and through the preservation of soil C during forest fires (Figure 5).

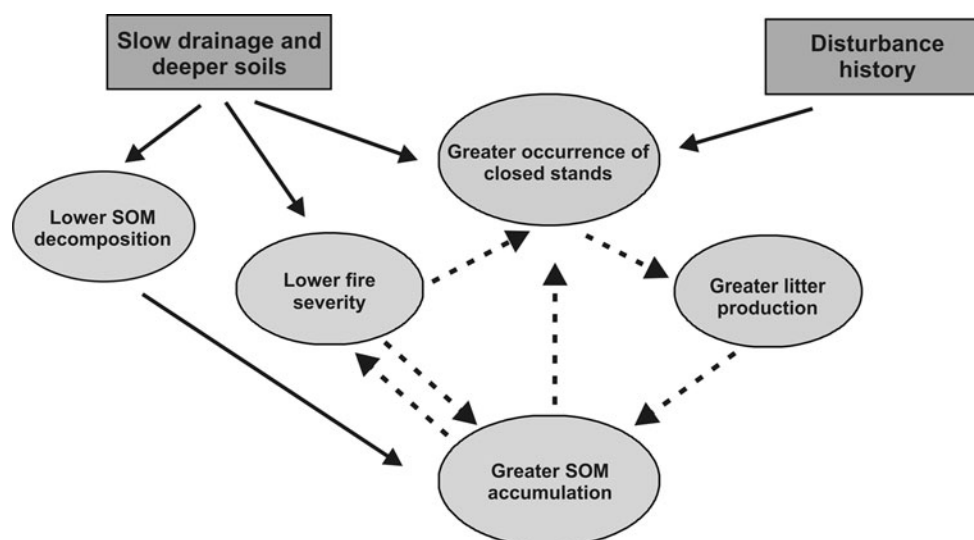


Figure 5. Schematic illustrations of factors contributing to greater soil organic matter (SOM) accumulation in upland closed forest stands. External drivers are indicated by *boxes*, whereas positive feedback loops are indicated by *dotted arrows*. The opposite relationships would be found for open-canopy vegetation types. The factors maintaining greater SOM in closed forest types could be responsible for the small variability of SOM quality across vegetation types as they would contribute to maintaining a positive relationship between fresh litter input to the soil and soil C stocks among vegetation types. Open stands should have a small litter input that is diluted into a small soil C reservoir, whereas closed forest stands would show a large fresh C litter input diluted into a large soil C reservoir. Fresh (young) litter inputs are thought to be responsible for most of the labile or active soil C.

Interestingly, in a recent study, Mansuy and others (2010) observed that the influence of site characteristics on fire frequency was calibrated by fire regime: site characteristics had no effect on fire frequency in regions experiencing a high fire frequency, such as the one covered in this study, although relationships were found in regions experiencing long fire cycles. The poor relationships between physical site characteristics and vegetation types in our study could thus be related to the high fire frequency experienced in the study area.

To sum up, stands with closed forest vegetation, although they were found on a wide range of drainage conditions, tended to be more abundant in slower drainage conditions. These stands contained greater soil C stocks and also supported more productive forests, perhaps because they are more resilient to severe disturbance and because their inherent productive capacity is higher. Positive feedback loops through C cycling would contribute to maintaining the association of greater soil C stores and closed vegetation types at the landscape level (Figure 5). The consideration of sites with poor drainage, namely sites undergoing paludification, as well as regions with longer fire cycles would bring different dynamics as open-canopy forests would be found on soils with a thicker organic layer (Simard and others 2007), and the

relationships found here would probably not be valid. Also, in this study, we did not control for the effect of stand age, which ranged between 22 and 101 years for OC, CC, and DEC stands. With time since fire, soil organic matter accumulates; however, the rate of accumulation is usually slow in boreal forests compared with C stocks, and highly variable (O'Neill and others 2006; Pregitzer and Euskirchen 2004). Because of the high fire frequency, the range of stand ages was limited in this study, and factors such as drainage and fire severity appeared to be playing a greater role than stand age in explaining soil C stocks as no relationships with stand age and organic layer C content within stand types could be found (data not shown).

Soil OM Properties

The organic layer C:N ratio was the only property of soil organic matter that contrasted between vegetation types. Its low values in deciduous stands suggest that these stands may cycle much more N relative to C. Lovett and others (2002) also observed a strong influence of tree species composition on the soil C:N ratio, with consequences for N leaching.

Besides the soil organic layer C:N ratio, very little difference in soil organic matter quality existed between vegetation types, which was somewhat

surprising. A higher proportion of labile organic matter in deciduous compared with coniferous stands was reported by Rey and Jarvis (2006) as well as Côté and others (2000), whereas other studies reported the opposite trend (Giardina and others 2001) or no clear distinction (Paré and others 2006). In this study, we anticipated a low proportion of mineralizable C in recently burned sites because it has been observed that such sites are enriched in recalcitrant C forms that are more resistant to microbial degradation (Thiffault and others 2008). It was therefore surprising that there were no significant differences between vegetation types in the cumulative specific mineralized C and that recently burned sites showed relatively high values. A possible explanation for the absence of differences in soil organic matter quality between vegetation types is that the most productive types are those where the soil has the capacity to accumulate more C in a stable form and therefore where a relatively large fresh annual C input is diluted into a large stable C pool, contrary to open vegetation types where a small C input is diluted into a small total C pool (Figure 4). Such an association between soil C stocks and vegetation productivity may not occur in all landscapes. In boreal landscapes, where poor drainage often limits forest growth, the opposite is commonly observed. For example, Légaré and others (2005), in boreal mixedwood forests, and Simard and others (2007), in paludified forests, found the opposite trend with a greater organic layer depth in less productive stands. These conditions would favor a lower organic matter quality in sites with higher organic matter accumulation, as was observed by Côté and others (2000).

Soil Heterotrophic Respiration

The variability in estimated soil heterotrophic respiration across vegetation types is caused by differences in both total soil C stores and organic matter quality. Because soil organic matter content was much more contrasted between vegetation types than soil organic matter quality, the difference in soil heterotrophic respiration rates can be explained to a great extent by differences in C stocks, which varied more than 2-fold across vegetation types. On the other hand, the contribution of soil organic matter quality to explaining differences in soil heterotrophic respiration rates is minor as it varied at most by 30% from the lowest to the highest values of the different soil C quality indicators presented in Table 2. The small variability in soil C quality found in the present landscape, as expressed by the

proportion of mineralized C on total C as well as by *Q10* values, could help simplify the modelling of soil C fluxes in this environment because estimates of soil C stores would explain much of the soil C flux variability.

CONCLUSION

At the regional scale, our results suggest that easily mineralizable soil C stocks and, presumably, soil heterotrophic respiration are greatly related to the size of total soil C stocks. These stocks are more important in deciduous and coniferous closed canopy types than in other open-canopy vegetation types. The soils of these vegetation types are thus more likely to release greater CO₂ fluxes into the atmosphere than the other vegetation types considered in this study given an interruption in tree productivity caused by disturbances or flooding. Nevertheless, because of their low representativeness in the territory studied (6%) compared with the open canopy and burned vegetation types, which represented altogether more than 50% of the territory, the potential for C loss from these vegetation types remains low at the landscape scale. Our results also suggest that the expansion of open woodlands within closed-crown forests (Girard and others 2008) would generate a landscape in which C exchange through the soil should be lower. Also, because the organic layer contains more C than the mineral soil, changes in fire frequency and fire severity would strongly affect soil C storage.

ACKNOWLEDGMENTS

This research was conducted in collaboration with the EM-1 Reservoirs' net greenhouse gas emission group financed by Hydro-Québec and thanks to a graduate scholarship to J. L. Banville from the Natural Sciences and Engineering Research Council of Canada. We are grateful to GEOTOP UQAM-MCGILL and the Canadian Forest Service for providing technical support as well as field assistants. We thank Jacques Morissette, Robert Boutin, Luc Pelletier and Luc St-Antoine for their advice and precious help and André Robitaille of the Ministère des Ressources naturelles et de la faune du Québec for access to the data of the programme d'inventaire écoforestier nordique.

REFERENCES

- Bellamy PH, Loveland PJ, Bradley RI, Lark RM, Kirk GJD. 2005. Carbon losses from all soil across England and Wales 1978–2003. *Nature* 437:245–8.

- Bhatti JS, Apps MJ, Jiang H. 2002. Influence of nutrients, disturbances and site conditions on carbon stocks along a boreal forest transect in central Canada. *Plant Soil* 242:1–14.
- Bhatti JS, van Kooten GC, Apps MJ, Laird LD, Campbell ID, Campbell C, Turetsky MR, Yu Z, Banfield E. 2003. Carbon balance and climate change in boreal forests. In: Burton PJ, Messier C, Smith DW, Adamowicz WL, Eds. *Towards sustainable management of the boreal forest*. Ottawa: NRC Research Press. p 799–855.
- Borken W, Xu YJ, Davidson EA, Beese F. 2002. Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. *Glob Change Biol* 8:1205–16.
- Callesen I, Liski J, Raulund-Rasmussen K, Olsson MT, Taustrand L, Vesterdal L, Westman CJ. 2003. Soil carbon stores in Nordic well-drained forest soils—relationships with climate and texture class. *Glob Change Biol* 9:358–70.
- Canadell JG, Pataki DE, Gifford R, Houghton RA, Luo Y, Raupach MR, Smith P, Steffen W. 2007. Saturation of the terrestrial carbon sink. In: Canadell JG, Pataki D, Pitelka L, Eds. *Terrestrial ecosystems in a changing world*. The IGBP Series. Berlin: Springer. p 59–74.
- Carter MR. 1993. *Soil sampling and methods of analysis*. Boca Raton: Lewis Publishers.
- Côté L, Brown S, Paré D, Fyles J, Bauhus J. 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. *Soil Biol Biochem* 32:1079–90.
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184–7.
- CSSC (Canada Soil Survey Committee). 1998. *The Canadian System of Soil Classification*, 3rd edn, Publ. no 1646e. Agriculture and Agri-Food Canada, Ottawa, Canada. http://sis.agr.gc.ca/cansis/references/1998sc_a.html.
- Dalias P, Anderson JM, Bottner P, Coûteaux M-M. 2001. Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. *Glob Change Biol* 7:181–92.
- Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–73.
- Epting J, Verbyla D. 2005. Landscape-level interactions of prefire vegetation, burn severity, and postfire vegetation over a 16-year period in interior Alaska. *Can J For Res* 35:1367–77.
- Flannigan MD, Bergeron Y, Engelmark O, Wotton BM. 1998. Future wildfire in circumboreal forests in relation to global warming. *J Veg Sci* 9:469–76.
- Giardina CP, Ryan MG, Hubbard RM, Binkley D. 2001. Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Sci Soc Am J* 65:1272–9.
- Girard F, Payette S, Gagnon R. 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. *J Biogeogr* 35:529–37.
- Gower ST, Vogel JG, Norman JM, Kucharik CJ, Steele SJ, Stow TK. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J Geophys Res* 102: 29–41.
- Gower ST, Krankina O, Olson RJ, Apps M, Linder S, Wang C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol Appl* 11:1395–411.
- Grenier M, Labrecque S, Garneau M. 2008. Cartographie des milieux secs pour le territoire de la phase 1 du secteur de la rivière Eastmain. Accord de collaboration entre Hydro-Québec et Environnement Canada 6161-5-0412. p 30.
- Harden JW, Trumbore SE, Stocks BJ, Hirsch A, Gower ST, O'Neill KP, Kasischke ES. 2000. The role of fire in the boreal carbon budget. *Glob Change Biol* 6(Supp 1):174–84.
- Hoey TB. 2004. The size of sedimentary particles. In: Evans DJA, Benn DI, Eds. *A practical guide to the study of glacial sediments*. London: Oxford University Press. p 54–77.
- IPCC (Intergovernmental Panel on Climate Change). 2001. Chapter 1: Global perspectives. In: Watson RT, Nobel IR, Bolin B, Ravindranath NH, Verardo DJ, Dokken DJ, Eds. *Land use, land-use change and forestry*. Cambridge: Cambridge University Press. p 550.
- Jasinski JPP, Payette S. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. *Ecol Monogr* 75:561–83.
- Johnstone JF, Chapin FSIII, Hollingsworth TN, Mack MC, Romanovsky V, Turetsky M. 2010. Fire, climate change, and forest resilience in interior Alaska. *Can J For Res* 40:1302–12.
- Kirschbaum MUF. 2006. The temperature dependence of organic-matter decomposition—still a topic of debate. *Soil Biol Biochem* 38:2510–18.
- Knorr W, Prentice IC, House JI, Holland EA. 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature* 433:298–300.
- Kurz WA, Apps M. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol Appl* 9: 526–47.
- Kurz WA, Apps M, Banfield E, Stinson G. 2002. Forest carbon accounting at the operational scale. *For Chron* 78:672–9.
- Kurz WA, Stinson G, Rampley GJ, Dymond CC, Neilson ET. 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proc Natl Acad Sci USA* 105:1551–5.
- Ladegaard-Pedersen P, Elberling B, Vesterdal L. 2005. Soil carbon stocks, mineralization rates, and CO₂ effluxes under 10 tree species on contrasting soil types. *Can J For Res* 35: 1277–84.
- Le Goff H, Girardin MP, Flannigan MD, Bergeron Y. 2008. Dendroclimatic inference of wildfire activity in Quebec over the 20th century and implications for natural disturbance-based forest management at the northern limit of the commercial forest. *Int J Wildl Fire* 17:348–62.
- Leboeuf A, Létourneau J-P, Robitaille A, Matejek S. 2009. Guide de stratification écoforestière. Programme d'inventaire écoforestier nordique. Ministère des Ressources naturelles et de la Faune du Québec. 29 p.
- Légaré S, Paré D, Bergeron Y. 2005. Influence of aspen on forest floor properties in black spruce-dominated stands. *Plant Soil* 275:207–20.
- Liski J, Ilvesniemi H, Mäkelä A, Westman CJ. 1999. CO₂ emissions from soil in response to climate warming are overestimated—The decomposition of old organic matter is tolerant of temperature. *Ambio* 28:171–4.
- Lovett GM, Weathers KC, Arthur MA. 2002. Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. *Ecosystems* 5:712–18.
- Manies KL, Harden JW, Yoshikawa K, Randerson J. 2001. The effect of soil drainage on fire and carbon cycling in Central Alaska. U.S. Geol Surv Prof Paper 1678:145–52.

- Mansuy N, Gauthier S, Robitaille A, Bergeron Y. 2010. The impact of surficial deposit-drainage combinations associated with physical factors on spatial variations of fire cycle in northern Quebec, Canada. *J Wildl Fire* 19:1083–98.
- McLauchlan KK, Hobbie SE. 2004. Comparison of labile soil organic matter fractionation techniques. *Soil Sci Soc Am J* 68:1616–25.
- Melillo JM, Steudler PA, Aber JD, Newkirk K, Lux H, Bowles FP, Catricala C, Magill A, Ahrens T, Morrisseau S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298:2173–6.
- O'Neill KP, Richter DD, Kasischke ES. 2006. Succession-driven changes in soil respiration following fire in black spruce stands of interior Alaska. *Biogeochemistry* 80:1–20.
- Paré D, Boutin R, Larocque GR, Raulier F. 2006. Effect of temperature on soil organic matter decomposition in three forest biomes of eastern Canada. *Can J Soil Sci* 86:247–56.
- Parton WJ, Schimel DS, Cole CV, Ojima DS. 1987. Analysis of the factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci Soc Am J* 51:1173–9.
- Paul EA, Morris SJ, Böhm S. 2001. The determination of soil C pool sizes and turnover rates: biophysical fractionation and tracers. In: Lal R, Kimble JM, Follett RF, Stewart BA, Eds. *Assessment methods for soil carbon*. Boca Raton: Lewis Publishers. p 193–206.
- Paul KL, Polglase PJ, Nyakuengama JG, Khanna PK. 2002. Change in soil carbon following afforestation. *For Ecol Manag* 168:241–57.
- Paul EA, Morris SJ, Conant RT, Plante AF. 2006. Does the acid hydrolysis incubation method measure meaningful soil organic carbon pools? *Soil Sci Soc Am J* 70:1023–35.
- Payette S, Bhiry N, Delwaide A, Simard M. 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. *Can J For Res* 30:288–305.
- Pregitzer KS, Euskirchen ES. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Glob Change Biol* 10:2052–77.
- Rey A, Jarvis P. 2006. Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). *Glob Change Biol* 12:1894–908.
- Robitaille A, Saucier J-P. 1998. *Paysages régionaux du Québec méridional*. Sainte-Foy (Québec): Les Publications du Québec. p 213.
- Simard M, Lecomte N, Bergeron Y, Bernier PY, Paré D. 2007. Forest productivity decline caused by successional paludification of boreal soils. *Ecol Appl* 17:1619–37.
- Stanford G, Smith SJ. 1972. Nitrogen mineralization potentials of soils. *Proc Soil Sci Soc Am* 36:465–72.
- Thiffault E, Hannam KD, Quideau SA, Paré D, Bélanger N, Oh S-W, Munson AD. 2008. Chemical composition of forest floor and consequences for nutrient availability after wildfire and harvesting in the boreal forest. *Plant Soil* 308:37–53.
- Torn MS, Trumbore SE, Chadwick OA, Vitousek PM, Hendricks DM. 1997. Mineral control of soil organic carbon storage and turnover. *Nature* 389:170–3.
- Trumbore S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground dynamics. *Ecol Appl* 10:399–411.
- Trumbore SE, Chadwick OA, Amundson R. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* 272:393–6.
- Wilson CV. 1971. *Le climat du Québec, partie 1: atlas climatique*. Service météorologique du Canada, Études climatologiques no 11.
- van Bellen S, Dallaire P-L, Garneau, M, Bergeron, Y. 2011. Quantifying spatial and temporal holocene carbon accumulation in ombrotrophic peatlands of the Eastmain region, Quebec, Canada. *Glob Biogeochem Cycles*. doi:[10.1029/2010GB003877](https://doi.org/10.1029/2010GB003877).
- Yu Z, Apps MJ, Bhatti JS. 2002. Implications of floristic and environmental variation for carbon cycle dynamics in boreal forest ecosystems of central Canada. *J Veg Sci* 13:327–40.