Black Spruce Soils Accumulate More Uncomplexed Organic Matter than Aspen Soils

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Improving knowledge on the dynamics and maintenance of the boreal soil's C pool is of particular importance in response to climate change concerns. We hypothesized that different forest types (black spruce, trembling aspen, and mixedwood) found on a similar site type differentially affect soil organic carbon (SOC) distribution among physical fractions. The surface mineral soil (0–15 cm) of 24 plots differing in forest composition was sampled in forested Hapludalfs of the Abitibi-James Bay region, Canada. The soil was first separated into three water-stable aggregate size fractions (>1000, 1000–250, and <250 μm) by wet sieving, followed by a density flotation (NaI: 1.7 g cm^{-3}) and a dispersion (with glass beads) to isolate the free light fraction (LF), the intraaggregate particulate organic matter (iPOM) and the silt plus clay fraction (S&C). According to mixed linear models, whole SOC contents (in Mg C ha^{-1}) decreased in the following order: black spruce (46.3) > mixedwood (41.9) > trembling aspen (34.7). While similar amounts of SOC (~30 Mg C ha^{-1}) were found in the S&C, more SOC was found in the less protected fractions (i.e., uncomplexed organic matter, UOM: LF and iPOM) under black spruce than under trembling aspen, the mixedwood being intermediate. This higher accumulation of UOM under black spruce suggests a slower C turnover that is probably induced by the low-quality C inputs and environmental constraints to decomposition found in these forests. These differences in the amounts of SOC stored within soil physical fractions might have strong repercussions on the SOC budget of the boreal forest of eastern Canada under climate change.

Abbreviations: CEC, cation exchange capacity; HF, heavy fraction; iPOM, intraaggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction; SOC, soil organic carbon; UOM, uncomplexed organic matter.

Boreal soils hold one of the largest pools of terrestrial C in the form of SOC, storing around three times more SOC than temperate or tropical biomes (Lal, 2005). Accordingly, any variation in the size and turnover rate of this major C pool could alter atmospheric CO$_2$ concentration and global climate.

The residence time of C in soils is highly variable, ranging from a few days to thousands of years (von Lützow et al., 2006). Soil organic C stabilization and accumulation depend on a variety of factors, including C input rate and quality, and soil microclimatic conditions such as temperature and moisture that greatly affect the C output rate, that is, decomposition (Lorenz and Lal, 2010). Stabilization of SOC also occurs when organic matter and mineral particles are mixed together to form organo-mineral complexes. Tisdall and Oades (1982) conceptualized a hierarchical structure for soil aggregation that involves a distribution of organic matter into differently sized aggregates with varying degrees of stability. Interactions between organic matter, roots, microbes, and mineral particles generate macroaggregates (>250 μm) that contain C in various soil fractions, namely microbial biomass, free organic matter (e.g., LF), iPOM, and the S&C (Fig. 1). While the former fractions are generally considered to be relatively labile, C in iPOM would be physically protected from microbial degradation by occlusion within aggregates whereas C associated with S&C would be further protected by chemical association with mineral surfaces (Blanco-Canqui and Lal, 2004; von Lützow et al., 2006). As macroaggregates become older, they disrupt into several,

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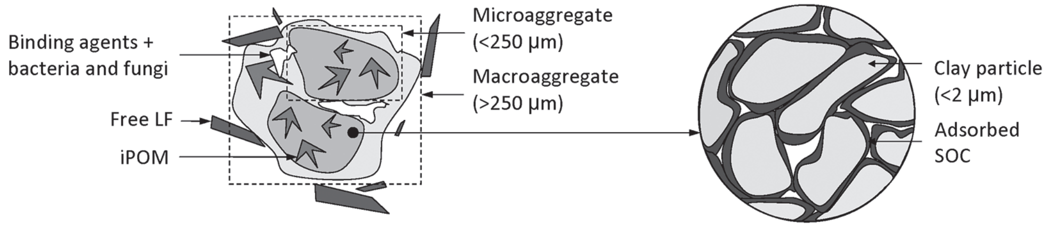

Free LF
Free and generally labile forms of SOC, e.g., residues of plants, animals, microorganisms

iPOM
SOC encapsulated in micro- and macro-aggregates

S&C
SOC chemically protected from microbial respiration via strong bonds

Fig. 1. Graphical representation and general description of the different soil physical fractions isolated in this study (iPOM, intraaggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction; SOC, soil organic carbon).

more stable fractions called microaggregates (<250 μm) (Angers et al., 1997), which may recombine into macroaggregates thereafter (Six et al., 2000).

The formation and stabilization of aggregates depend on abiotic factors such as soil mineralogy, texture, cation content and sesquioxides content (aluminum and iron oxides), as well as biotic factors such as organic matter quantity and quality, diversity and abundance of soil organisms, and especially the presence of macrofauna (Abiven et al., 2009; Bossuyt et al., 2006). Most of these variables are singularly affected by the nature of the forest cover, such as tree species composition (Binkley and Valentine, 1991; Flanagan and Van Cleve, 1983; Hobbie et al., 2006; Hodson and Sangster, 1999; Laganière et al., 2009). Hence, the stability of SOC stocks should vary according to tree species composition.

In the Canadian boreal forest, black spruce (*Picea mariana* [Mill.] BSP) is the most common tree species, covering more than 150 million ha (Canada's NFI, 2010). Black spruce forests accumulate large quantities of SOC in their forest floor and surface mineral layers in response to both poor litter quality (i.e., biochemical recalcitrance) and the cold and wet microclimatic conditions associated with this forest type that limit the activity of soil decomposers (Fenton et al., 2005; Laganière et al., 2009; Lavoie et al., 2005). Over the past century, we have observed an expansion of broadleaved tree species such as trembling aspen (*Populus tremuloides* Michx.) over a large area of the boreal forest that is probably induced by a change in the frequency of human and/or natural disturbances such as road construction, forest cutting activities, wildfire and insect outbreaks (Ilisson and Chen, 2009; Laquerre et al., 2009). The presence of aspen patches within black spruce-dominated forests has been related to better litter quality and enhancement of soil microclimatic conditions, resulting in attendant increases in soil biological activity and decomposition rates (Laganière et al., 2009, 2010a; Légaré et al., 2005). Consequently, an increase in the relative abundance of aspen at the landscape level may have implications in terms of SOC storage and stability. While the effect of black spruce and aspen on C stabilization through litter quality and soil microclimate is well understood, how these two tree species affect C stabilization through soil aggregation and soil physical fractions is unknown. Improving knowledge on the dynamics and maintenance of such a major C pool is of particular importance in response to climate change concerns and greenhouse gas mitigation efforts (Cole et al., 1996).

The aim of this study was to explore the influence of black spruce and trembling aspen, either in pure stands or in mixtures, on C distribution among soil aggregate size classes and soil physical fractions. The proportions and contents of C associated with LF, iPOM, and S&C were determined in forested Hapludalfs of the eastern Boreal Shield, Canada. The proportions of C contained within water-stable macro- and microaggregates were also determined. We hypothesized that the higher soil biological activity usually found under broadleaved tree species (Laganière et al., 2009) would be reflected by lower SOC content under aspen than under black spruce but a higher proportion of C protected inside aggregates (i.e., iPOM and S&C).

MATERIALS AND METHODS

Study Area and Sampling

The study area is located in the Eastern Boreal Shield of Canada, in the Abitibi-James Bay region of Quebec (49°08′ to 49°11′ N, 78°46′ to 78°53′ W). This region is part of the black spruce–feathermoss [*Pleurozium schreberi* (Brid.) Mitt.] forest of western Quebec (Grondin, 1996). This domain extends over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse, in the Wisconsinan glacial age (Vincent and Hardy, 1977). A large part of this region is characterized by homogeneous site conditions: a flat topography, a fine-textured parent material (~50% clay), and Hapludalf as the main soil type (Soil Survey Staff, 2006). The dominant disturbance type is large fires that kill all aboveground vegetation. The climate is boreal with a mean annual temperature of 0.7°C and annual precipitation of 890 mm (Environment Canada, 2010).

Eight mature forest sites dominated by black spruce and trembling aspen, each ranging from pure stands to a variety of mixtures of both species, were selected for the purpose of the study (for soil sampling). These sites were located in an area of 36 km^2 with a maximum distance of 7 km between sites. At each site, three 400 m^2 sampling plots were randomly established: one dominated by black spruce, one dominated by aspen, and the third one, mixed uniformly with both tree species. The vegetation under spruce canopy included mainly Labrador tea (*Ledum groenlandicum* Oeder), *Vaccinium* spp., and feathermoss; the latter was the dominant ground cover and an important input of organic matter to the soil (Bisbee et al., 2001). The aspen understory included herbs and isolated clumps of speckled alder [*Alnus rugosa* (Du Roi) Spreng.] while the mixedwood understory comprised a mixture of those found under spruce and aspen. The sampling plots were separated by a distance of 40 to 100 m to minimize variability within a site. All sites originated from the same fire that occurred in 1916 (Bergeron et al., 2004). During the selection of the sites, particular attention was given to ensuring the similarity of permanent site conditions (Tables 1 and 2). Thus, any variation in the dependent variables is assumed to be the effect of tree species and their associated understory. More information on stand characteristics is found in Cavard et al. (2010).

In October 2008, four surface mineral soil samples (0–15 cm depth) were carefully extracted from each plot with a metal corer (diam: 4.7 cm) and were pooled to yield one composite soil sample. The forest floor layer (LFH or O horizon) was removed before soil collection. Soil samples were placed in coolers and brought to the laboratory for further analysis. During sample collection and transportation, precautions were taken to avoid soil compaction and to minimize the crushing of soil aggregates.

Aggregate-Size Separation

The field-moist soil samples were gently broken along natural planes of weakness and passed through a 6-mm sieve before air-drying. Subsamples (2 × 100 g) of the air-dried soils were wet-sieved using the Kemper technique as described in Angers et al. (2007), giving three aggregate-size classes: >1000 µm fraction (large macroaggregates), 250–1000 ∝m fraction (small macroaggregates), and <250 µm fraction (microaggregates and S&C). Briefly, the soil was placed on a set of sieves (250 and 1000 ∝m) and soaked in deionized water before sieving for 10 min to allow slaking, which is the breaking of unstable aggregates due to air and pressure buildup inside the aggregates on submersion in water. By starting the motor of the wet-sieving apparatus, the sieves were allowed to raise and lower 3.9 cm, 30 times per min for 10 min. Material remaining on the sieves was rinsed into preweighed plastic pans. Material passing through the 250-∝m mesh was poured into 1-L plastic jars and centrifuged for 15 min at 2000 rpm to discard the excess water. The three aggregate-size fractions were oven-dried at 50°C and weighed.

Table 1. Site characteristics of the forest types located in the eastern boreal forest of Canada ($n = 8$). Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the Materials and methods section.

Site characteristics	Forest type		
	Spruce	Mixewood	Aspen
Topography	flat	flat	flat
Stand origin	wildfire (1916)	wildfire (1916)	wildfire (1916)
Climate	boreal	boreal	boreal
Mean annual temperature, °C†	0.7	0.7	0.7
Mean annual precipitation, mm	890	890	890
Drainage	moderate	moderate	moderate
Parent material	lacustrine clay	lacustrine clay	lacustrine clay
Soil type	Hapludalf	Hapludalf	Hapludalf
Soil texture	clayey	clayey	clayey
Basal area		%	
Spruce‡	89.4 ± 4.2a	33.8 ± 3.6b	8.9 ± 1.8c
Aspen	1.8 ± 0.7c	59.5 ± 3.5b	88.5 ± 2.6a
Other species	8.8 ± 4.0ab	6.7 ± 1.6a	2.6 ± 2.3b
C stock§		t ha^{-1}	
Forest floor	41.4 ± 2.66a	31.3 ± 1.74b	23.5 ± 1.35c
Mineral soil 0–15 cm	43.9 ± 4.78a	37.0 ± 3.77ab	33.6 ± 3.61b
Mineral soil 15–55 cm	45.4 ± 16.4a	40.5 ± 12.9a	54.9 ± 18.9a

† Mean annual temperature and precipitation are from Environment Canada (2010).

‡ Tree basal areas are means ± 1 SE from Cavard et al. (2010).

§ Forest floor and mineral soil C stocks are means ± 1 SE from J. Laganière (2010, unpublished data).

Density Fractionation and Aggregate Dispersion

Free LF organic matter was separated from the heavy fraction (HF) (i.e., mineral soil) by density flotation following the method described in Gregorich and Beare (2007). Briefly, a subsample (20 g) of each of the three different aggregate-size classes was soaked in 1.7 g cm^{-3} sodium iodide (NaI), slowly shaken by hand, and allowed to settle for 48 h before recovering the suspended LF with a vacuum filtration unit equipped with a 0.45-µm nylon filter. The 1.7 specific gravity is recommended for isolating LF as this density separates most organomineral and mineral particles from free organic materials (Gregorich and Beare, 2007). The LF was rinsed using a 0.01 M CaCl$_2$ solution

Table 2. Soil properties (means and 95% confidence limits) of the 0- to 15-cm mineral layer under different forest types located in the eastern boreal forest of Canada ($n = 8$). Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the Materials and methods section.

Soil characteristics	Forest type		
	Spruce	Mixewood	Aspen
C content, Mg C ha^{-1}	46.3 (36.6–58.6)a	41.9 (33.1–52.9)ab	34.7 (27.5–43.9)b
N content, Mg C ha^{-1}	2.5 (2.1–2.9)a	2.5 (2.1–3.1)a	2.4 (2.0–2.8)a
Total C, g C kg^{-1}	37.5 (24.5–57.5)a	36.0 (22.4–58.0)a	26.6 (17.4–40.8)a
Total N, g N kg^{-1}	2.0 (1.4–2.9)a	2.2 (1.4–3.4)a	1.8 (1.2–2.7)a
C to N ratio	18.8 (17.3–20.5)a	16.5 (15.0–18.2)b	14.6 (13.4–15.9)c
Bulk density, g cm^{-3}	0.8 (0.7–1.0)a	0.8 (0.6–1.0)a	0.9 (0.7–1.1)a
pH (H_2O)	4.3 (4.1–4.6)b	4.6 (4.3–4.9)ab	4.7 (4.5–5.0)a
CEC, cmol(+) kg^{-1}	8.9 (6.8–12.0)a	8.7 (6.3–12.0)a	7.9 (6.0–10.0)a
Sand, %	10.6 (6.17–13.8)a	13.7 (6.84–21.0)a	13.7 (8.43–18.6)a
Silt, %	43.4 (37.9–48.7)a	39.8 (34.8–44.8)a	39.2 (33.9–43.7)a
Clay, %	46.0 (39.6–52.4)a	46.5 (38.8–55.5)a	45.9 (39.5–51.9)a

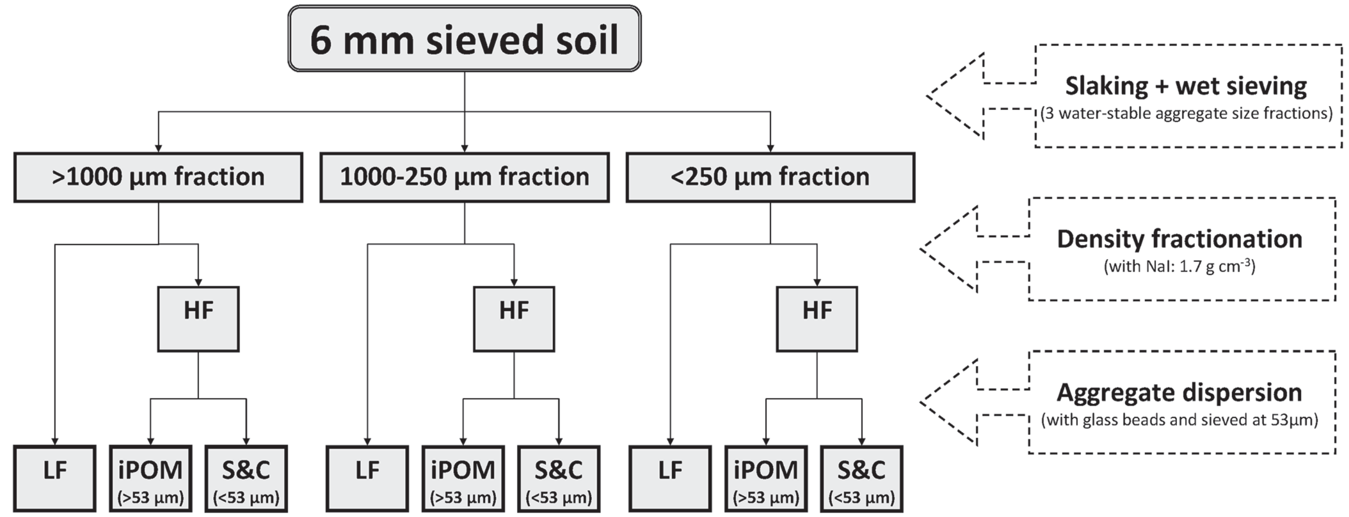

Fig. 2. Soil fractionation scheme used in this study (HF, heavy fraction; iPOM, intraaggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction).

and deionized water, oven-dried at 50°C, and weighed. The HF was rinsed as described above and centrifuged for 15 min at 2000 rpm. This rinse-centrifugation cycle was repeated three to five times, until the supernatant became clear of NaI (uncolored). The HF was oven-dried at 50°C and weighed.

The iPOM was separated from the S&C by shaking the HF on a reciprocal shaker with 100 mL of deionized water and 10 glass beads for 16 h and by passing the dispersed fraction through a 53-∝m sieve. The material remaining on the sieve (i.e., iPOM) and the material passing through the 53-∝m meshes (i.e., S&C) were oven-dried at 50°C and weighed. Mass and organic C balances of all isolated soil fractions were used to determine recovery efficiency. A graphical representation of the soil fractionation scheme is shown in Fig. 2.

Soil Analyses

Subsamples from all fractions were ground and analyzed for their C and N concentrations by dry combustion using a LECO CHN-1000 analyzer (Leco Corp., St. Joseph, MI). No carbonates were detected in soil samples, thus the C analysis was a measure of total organic C concentration. The C content of each soil fraction was calculated and data were reported on a whole soil C basis. Cation exchange capacity (CEC) of whole soil was determined by summing exchangeable cations extracted with 0.1 M $BaCl_2$ and by atomic-absorption spectrophotometry (Hendershot et al., 2007). The pH was determined in water using a PHM82 pH meter (Radiometer, Copenhagen, Denmark) using a 1:2 soil:water ratio. Soil texture was determined using the standard hydrometer method (Kroetsch and Wang, 2007). The C saturation level of the S&C was calculated according to Carter et al. (2003).

Statistical Analysis

The data were analyzed using the MIXED procedure of SAS System v.9.1 (SAS Institute Inc., Cary, NC). Forest type and soil properties or size-density fraction were considered as fixed effects whereas site and replication (nested within site) were considered as random effects. The mixed model is written as follows: $\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\gamma + \varepsilon$; where $\mathbf{y}$ represents a vector of observed data, β is an unknown vector of fixed-effects parameters with known design matrix $\mathbf{X}$, γ is an unknown vector of random-effects parameters with known design matrix $\mathbf{Z}$, and ε is an unknown random error vector. To meet the assumptions of normality and homoscedasticity, the data were log10-transformed (soil properties) or arcsine-transformed (soil size-density fraction). The analysis was weighted (WEIGHT statement) by a measure of tree species composition to minimize the impact of unwanted tree species in a sampling plot. Thus, a "pure aspen" plot containing 100% of aspen had a higher weight than one containing 95% of aspen and 5% of other species (unwanted). The WEIGHT statement operates by replacing $\mathbf{X}'\mathbf{X}$ and $\mathbf{Z}'\mathbf{Z}$ with $\mathbf{X}'\mathbf{W}\mathbf{X}$ and $\mathbf{Z}'\mathbf{W}\mathbf{Z}$, where $\mathbf{W}$ is the diagonal weight matrix. Differences between means were tested using orthogonal contrasts (CONTRAST statement). For result presentation, means (estimates) and confidence limits were converted back to the original scale by reversing the transformation. Statistical significance was set up at the 0.05 level, but significant difference at the 0.10 level was also considered given the inherent large variability in forest soils.

RESULTS

To ensure that potential losses during the fractionation procedure did not introduce bias, the mass and organic C content of the whole soil were compared with the sums of mass and C content in the various fractions to determine recovery efficiency. Calculations of the mass and C balances revealed that recovery efficiency was on average (±1 SE) 99.3 (±0.4)% and 95.0 (±2.0)%, respectively (data not shown). The reproducibility of separation procedures was on average (±1 SE) 91.9 (±0.5)% (data not shown).

Whole Soil Characteristics

Differences in C content and C to N ratio among forest types decreased in the following order: black spruce (46.3 Mg C ha^{-1}, 18.8) > mixedwood (41.9 Mg C ha^{-1}, 16.5) > trembling aspen (34.7 Mg C ha^{-1}, 14.6); no significant difference was found for N content, total C and total N (Table 2). Soil pH was significantly higher under aspen (4.7) than under spruce (4.3), and intermediate under mixedwood (4.6). Bulk density, CEC and soil texture were not different among forest types (Table 2).

Carbon Distribution in the Aggregate Sizes

Aggregate C content of the mineral soil decreased in the following order: large macroaggregate (>1000 μm) > small macroaggregate (1000–250 μm) > microaggregate and S&C (<250 μm) (Fig. 3). Around 85% of total C content was found in the macroaggregate fraction (55% in the large macroaggregate fraction and 30% in the small macroaggregate fraction), and only 15% was found in the microaggregate and S&C. The proportions of total C content within these aggregate size classes were not different among forest types (Fig. 3). Similar results were found for soil weight partition among aggregate size classes (data not shown).

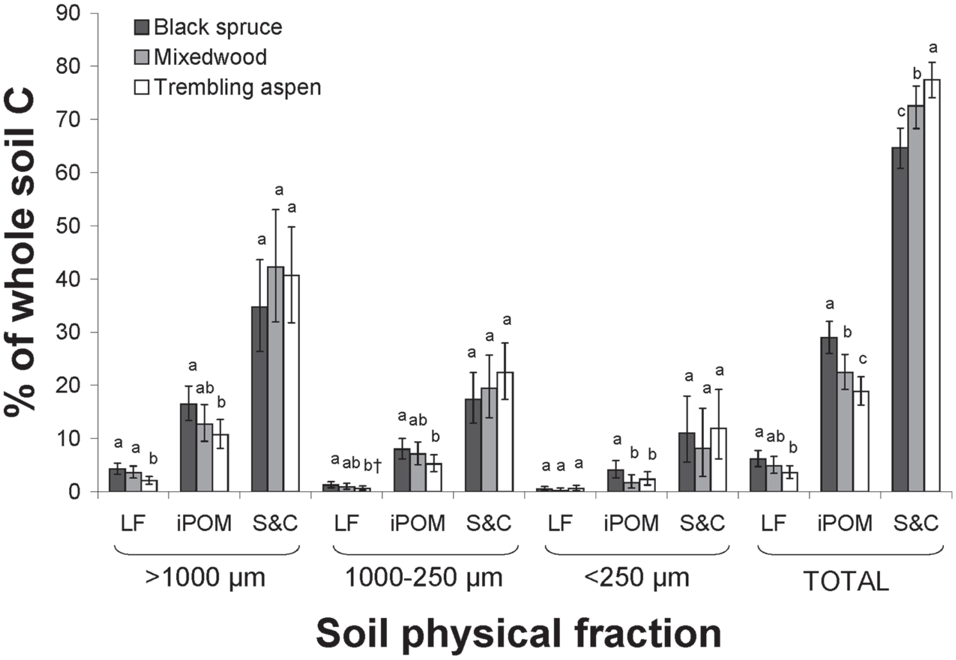

Fig. 4. Proportions of total C content (means and 95% confidence limits) stored within soil size-density fractions among forest types (iPOM, intraaggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction). Different lowercase letters denote significant differences at $p < 0.05$ (†, $p < 0.10$) between forest types according to the mixed linear models as described in the *Materials and Methods* section.

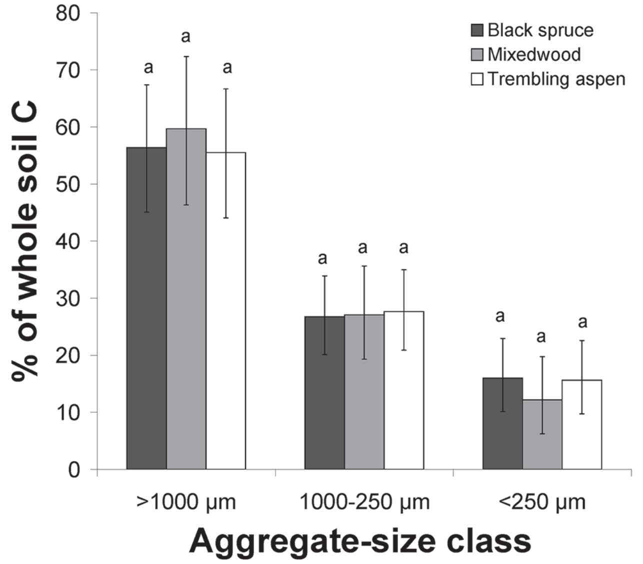

Fig. 3. Proportions of total C content (means and 95% confidence limits) stored within aggregate size classes among forest types. Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the *Materials and Methods* section.

Carbon Distribution in the Size-Density Fractions

The proportions of total C content and the C contents stored (in Mg C ha^{-1}) within size-density fractions were significantly different among forest types (Fig. 4 and 5). In general, more C was found in LF and iPOM under spruce (6.13% or 2.67 Mg C ha^{-1} and 28.94% or 13.32 Mg C ha^{-1}, respectively) than under aspen (3.61% or 1.23 Mg C ha^{-1} and 18.87% or 6.47 Mg C ha^{-1}, respectively), the values under

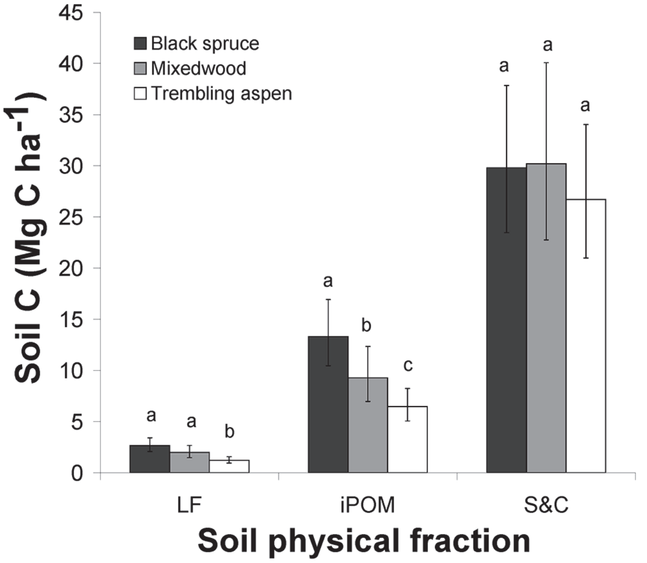

Fig. 5. C content (means and 95% confidence limits) stored within soil size-density fractions among forest types (iPOM, intraaggregate particulate organic matter fraction; LF, light fraction; S&C, silt plus clay fraction). Different lowercase letters denote significant differences at $p < 0.05$ between forest types according to the mixed linear models as described in the *Materials and Methods* section.

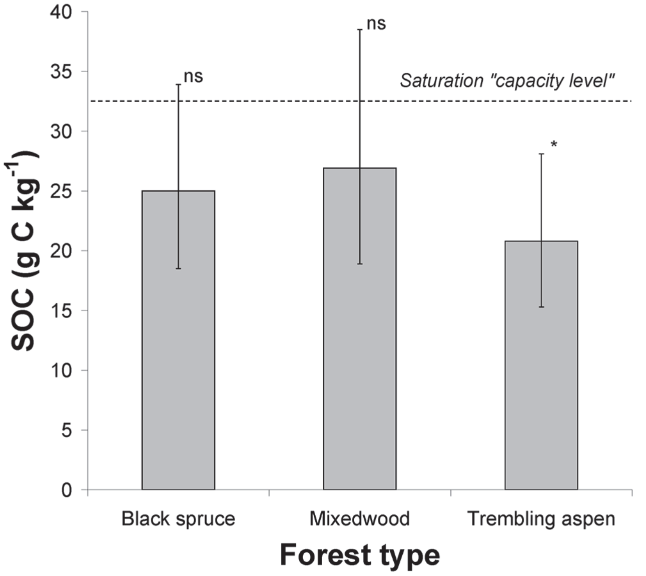

Fig. 6. Comparison between mineral-associated C (means and 95% confidence limits) among forest types and C saturation level calculated according to Carter et al. (2003) (*, $p < 0.05$; ns, nonsignificant).

mixedwood being intermediate (4.90% or 2.00 Mg C ha^{-1} and 22.45% or 9.29 Mg C ha^{-1}, respectively). On a proportion basis only, more C was found in S&C under aspen and mixedwood than under spruce (Fig. 4).

Carbon Saturation Capacity

The C associated with mineral particles (S&C) was not significantly different from the theoretical capacity of soil C saturation in this fraction (Carter et al., 2003), except for trembling aspen soil where this fraction was significantly lower (Fig. 6). The S&C was saturated at 76%, 84 and 65% of the capacity level under black spruce, mixedwood and trembling aspen, respectively. The C saturation capacity of the soil fine fraction for the study area was estimated at 32.4 g C kg^{-1} (Fig. 6).

DISCUSSION

Because permanent site conditions such as drainage, soil texture, topography, stand origin, parent material and soil type were not related to tree species composition (Tables 1 and 2), the differences observed among soil physical fractions are attributed to the effect of tree species and their associated understory. To the best of our knowledge, this study is the first to specifically address the effect of forest types on SOC stabilization through soil aggregation and soil physical fractions in a natural ecosystem. The very few studies focusing on this topic took place in managed plantation systems (e.g., Blanco-Canqui et al., 2007; Gama-Rodrigues et al., 2010; Quideau et al., 1998; Saha et al., 2010; Sarkhot et al., 2008), where soil disturbance is high and naturally-associated understory is generally lacking. In addition, the tree species selected in these studies were mostly genetically improved species [e.g., loblolly pine (*Pinus taeda* L.) and hybrid poplar clones]. Under these relatively artificial conditions, most of these studies reported changes in soil aggregation or in soil physical fractions among tree species composition, even at the genotypic level.

Similarly, our findings highlight the potential of tree species and their associated understories to influence SOC stabilization in the Canadian boreal forest through soil physical fractions. While C distribution in the aggregate size classes was not different among forest types, C distribution among size-density fractions varied significantly. The amounts of C in LF and iPOM were higher under black spruce than other forest types, which was not expected. Because these soil fractions are not intimately bound to mineral particles, they can be defined as UOM (Christensen, 2001). Uncomplexed organic matter is believed to be less protected against microbial degradation compared with the mineral-associated fraction because it is more accessible to microbes and their enzymes, and usually less recalcitrant biochemically (von Lützow et al., 2006). In soils with permanent vegetation, UOM can represent from 15 to 40% of the SOC stored in the surface soil (Christensen, 2001). In our study, UOM accounted for 35%, 27 and 22% of total SOC under black spruce, mixedwood and aspen, respectively. Thus, black spruce forests accumulated more SOC in the less protected soil fractions relative to aspen.

While total SOC contents in the surface mineral layer were higher under black spruce (46.3 Mg C ha^{-1}), followed by mixedwood (41.9 Mg C ha^{-1}) and aspen (34.7 Mg C ha^{-1}), SOC contents associated with mineral particles (S&C) were similar among forest types, that is, about 30 Mg C ha^{-1}. The mineral-associated fraction has been referred to as passive fraction, owing to the chemical protection of adsorbed soil C at mineral surfaces (Fig. 1; Six et al., 2002). Together with secondary recalcitrance (e.g., black carbon), chemical protection is among the most efficient stabilization mechanisms for long-term C sequestration, with an estimated mean residence time of hundreds of years in the soil (Laird, 2001; Torn et al., 1997; Trumbore et al., 1996; von Lützow et al., 2006). Therefore, this implies that perhaps a large part of the C stored in this fraction does not originate from the current forest type.

It has been suggested that mineral soils have a limited capacity to store C in the fine fraction (Hassink, 1997). According to the C saturation theory, once the capacity level of the mineral-associated pool is reached, extra organic C accumulates in the UOM pool. A number of experiments corroborate this theory (e.g., Carter et al., 2003; Gulde et al., 2008; Hassink, 1997; Six et al., 2002). Although these studies were all conducted in agricultural systems, our study may also suggest a finite SOC storage capacity in forest soils, but this remains to be experimentally tested. While black spruce and mixedwood C levels were not different from the calculated C saturation level, the mineral-associated pool of aspen was significantly lower than the theoretical saturation level. Soils that were closer to the saturation level accumulated higher amounts of UOM (i.e., black spruce and mixedwood) compared with soils further away from saturation (i.e., aspen). Admittedly, a large variability may exist around this equation of soil saturation potential although, in relative terms, the results still suggest that black spruce and mixedwood were closer to saturation compared with aspen.

Differences among soil fractions in C distribution and in the soil saturation level reached may originate from differences in SOC mineralization rates between forest types. Furthermore, the higher accumulation of UOM under black spruce may indicate that these forests are characterized by a slower C turnover. Two main reasons may explain different C turnover rates between spruce and aspen. First, C inputs returned to the soil in black spruce forests come primarily from needle and moss litters that decompose slowly in the early stages of decomposition (Prescott et al., 2000; Van Cleve et al., 1986). Spruce litter is acidic, molecular-complex, and less palatable for soil decomposers compared with aspen broadleaves, while moss is made of simple but slow-decomposing compounds (Flanagan and Van Cleve, 1983; Van Cleve et al., 1986). Second, decomposition rates under spruce are typically slower because of harsh soil conditions limiting microbial activity (Fenton et al., 2005; Laganière et al., 2009; Lavoie et al., 2005). The soil under black spruce is colder than under aspen because light penetration to the forest floor and evapotranspiration capacity is lower, but mainly because the ground cover associated with black spruce (i.e., bryophytes) keeps the soil moist and insulated from thermal variations (Oechel and Van Cleve, 1986). These reasons may explain why more UOM was found under spruce relative to aspen and why soils under aspen were further away from saturation. Ecosystems that have environmental conditions constraining decomposition may have more UOM accumulating than what can be explained by C input alone (Gregorich et al., 2006). Consequently, the higher litter quality and the microclimatic conditions favoring decomposition under aspen may have reduced the amount of C available to enter either in LF, iPOM, the mineral-associated C pool or all three, thus reducing the soil saturation level as well as the amount of UOM.

What might happen to the different SOC pools following climate change is still uncertain and subject to speculation. The potential increase in soil temperature may reduce the environmental constraints on decomposition found under spruce and might cause losses of its extra amount of UOM. Otherwise, the main effect of climate change on SOC dynamics may not originate from changes in precipitation and temperature regimes, but may originate indirectly from variations in tree species composition and distribution (Fissore et al., 2009). If so, the replacement of black spruce with trembling aspen alone would result in a loss of around 25% of the total SOC contained in the surface mineral layer, which is worthy of consideration. In comparison, the conversion of forested lands to agricultural areas results in a depletion of SOC stocks by 30% on average (Laganière et al., 2010b).

CONCLUSION

Our results show that SOC stocks in the surface mineral layer were higher under black spruce than under mixedwood and aspen. A higher proportion of the SOC stock under aspen was chemically protected within S&C. On an absolute basis, however, the amounts of chemically-protected SOC did not differ with forest types (around 30 Mg C ha^{-1} each). Instead, the extra amounts of SOC contained in black spruce and mixedwood soils were present in the less protected fractions only (i.e., UOM: LF and iPOM), probably because these forests are characterized by slower C turnover and also because the capacity of these soils to chemically protect SOC on mineral surfaces was nearly reached. These differences in the amounts of SOC stored within soil physical fractions might have strong repercussions on the C budget of the Canadian boreal forest under climate change.

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