Stability of Soil Carbon Stocks Varies with Forest Composition in the Canadian Boreal Biome

Jérôme Laganière, David Paré, Yves Bergeron, Han Y. H. Chen, Brian W. Brassard & Xavier Cavard

Ecosystems

ISSN 1432-9840

Ecosystems
DOI 10.1007/s10021-013-9658-z

Springer

Your article is protected by copyright and all rights are held exclusively by Her Majesty the Queen in Right of Canada. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Author's personal copy

Ecosystems
DOI: 10.1007/s10021-013-9658-z

ECOSYSTEMS

© 2013 Her Majesty the Queen in Right of Canada

Stability of Soil Carbon Stocks Varies with Forest Composition in the Canadian Boreal Biome

Jérôme Laganière,[1,2,3]* David Paré,[1] Yves Bergeron,[2,3] Han Y. H. Chen,[4] Brian W. Brassard,[4] and Xavier Cavard[2,3]

[1]Natural 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; [2]Centre d'étude de la forêt, Université du Québec à Montréal, C.P. 8888, Succ. Centre-ville, Montreal, Quebec H3C 3P8, Canada; [3]NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 Boulevard de l'Université, Rouyn-Noranda, Quebec J9X 4E5, Canada; [4]Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1, Canada

ABSTRACT

Changes in forest composition as a result of forest management, natural disturbances, and climate change may affect the accumulation of soil organic carbon (SOC). We examined the influence of common boreal tree species (trembling aspen, black spruce, and jack pine), either in pure stands or in conifer-broadleaf mixtures, on the amount, distribution, and quality of SOC in two regions of the Canadian boreal biome. Long-term laboratory incubations were used to assess SOC quality by quantifying proportions of fast carbon (C) (that is, proportion of total C released during the first 100 days of incubation) and active C (that is, modeled proportion of total C that can be potentially released). Total amounts of SOC did not differ between stand types, but the effects of stand type on SOC stocks and quality differed with soil depth. Among stand types, aspen stands had the greatest relative proportion of total SOC in deeper mineral layers and the lowest amount of active C in the organic layer. For these reasons, the SOC stock that developed under aspen was more stable than in the other stand types. Although black spruce stands allowed a greater accumulation of SOC in surface layers, these stocks, however, might become more vulnerable to extra losses if environmental conditions are to become more favorable to decomposition in the future. Our work highlights that boreal forest composition influences the stability of SOC stocks and how climate change could alter this large C pool.

Key words: boreal forest; tree species; forest floor; mineral soil; organic matter quality; carbon stability; decomposition.

INTRODUCTION

The boreal forest stores large amounts of carbon (C) through vegetation and soil, making this biome one of the greatest terrestrial carbon reservoirs, mainly in the form of soil organic C (SOC) (Lorenz and Lal 2010). Accumulation of SOC depends on the balance between C input (that is, litterfall and root turnover) and output rates (that is, decomposition). The residence time of C entering the soil system is

---

Received 19 November 2012; accepted 10 February 2013

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-013-9658-z) contains supplementary material, which is available to authorized users.

Author Contributions: All authors contributed to the study design. JL performed research and analyzed data, and all authors wrote the paper.

**Corresponding author; e-mail:* jerome.laganiere@hotmail.com

Published online: 21 March 2013

Author's personal copy

highly variable, ranging from a few days to thousands of years (von Lützow and others 2006). Long-term stability of SOC may occur not only when organic matter is mixed with mineral particles to form organo-mineral complexes (that is, soil aggregates), but also when organic matter quality or environmental conditions are unfavorable for microbial decomposition (von Lützow and others 2006). In the boreal forest, the general poor plant litter quality and low temperatures are responsible for the observable low microbial activity and decomposition rates, allowing SOC to accumulate (De Deyn and others 2008).

Across the boreal biome, there remains a relatively wide range of organic matter quality and microclimatic conditions as a result of the difference in forest composition. For example, soil may be colder and wetter under some shade-tolerant, evergreen *Abies* spp. and *Picea* spp. than shade-intolerant, deciduous *Betula* spp. and *Populus* spp., under similar permanent site conditions (Binkley 1995; Hart and Chen 2006; Hobbie and others 2006; Laganière and others 2012). Moreover, decomposition rates of leaf and root litter can differ among tree species and associated understory plant species due to their differences in nutrients, lignin, and the secondary metabolites (Berg 2000; Preston and others 2000). The production of acidic litter can even prevent the presence of macroinvertebrates that may either enhance the breakdown of organic matter, the formation and stabilization of soil aggregates in mineral layers, or both (Bossuyt and others 2005; Reich and others 2005; Laganière and others 2009). Furthermore, root structure and vertical distribution differ among tree species and may affect accumulation and stabilization of SOC along the soil profile (Strong and La Roi 1983; Jobbagy and Jackson 2000; Brassard and others 2013). Therefore, by generating specific soil microclimatic conditions, by producing leaf and root litter in variable amounts and quality, by influencing SOC distribution within the soil profile, and also by influencing SOC associations with mineral particles, tree species have the potential to influence the fate of C in soil.

Alteration of the boreal ecosystem dynamics may have strong implications for climate change mitigation efforts. Over the past century, for example, large areas of the boreal forest have been converted from coniferous forests to broadleaved forests dominated by trembling aspen (*Populus tremuloides* Michx.) as a result of changes in the size and the frequency of disturbances including forest harvesting activities, insect outbreaks, and wildfires (Bond-Lamberty and others 2007; Soja and others 2007; Ilisson and Chen 2009). This phenomenon is particularly critical for the maintenance of boreal SOC stocks, given that trembling aspen forests, for example, store less SOC compared with black spruce forests (*Picea mariana* Mill. BSP) (Gower and others 2000; Vance and Chapin 2001; Laganière and others 2011), the most widespread stand type in the Canadian boreal forest (Canada's NFI 2010). In addition to changes in forest composition, SOC stocks of the boreal biome might be particularly vulnerable to global warming because a stronger temperature increase is anticipated in northern latitudes compared with the global average (IPCC 2007). Given the inherent temperature dependence of organic matter decomposition, SOC stocks might decrease under climate warming if not compensated for with a greater net primary production or with a decrease in the quality (decomposability) of litter produced (Lorenz and Lal 2010).

Surprisingly, few studies have examined the influence of forest composition on the amount and stability of soil C stocks in boreal forest ecosystems. A review by Jandl and others (2007) highlighted the necessity to differentiate SOC into labile and stable fractions among tree species. Owing to a lack of data, the effect of tree species composition on SOC storage in stable pools is questioned and still insufficiently proven (Jandl and others 2007). To accurately assess the impacts of recent and future ecosystem changes on the fate of the boreal SOC pool, we need to improve our knowledge of SOC dynamics as affected by forest composition.

The aim of this study was to examine the influence of common boreal tree species (two conifers: black spruce *Picea mariana* Mill. BSP and jack pine *Pinus banksiana* Lamb.; one broadleaf: trembling aspen *Populus tremuloides* Michx.; and conifer—trembling aspen mixtures), on the amount, distribution, and quality of SOC in two regions of the Canadian boreal biome. The amount and distribution of SOC were evaluated by sampling different layers of the soil profile (organic layer and 0–15, 15–35, and 35–55 cm layers of the mineral soil) for their C contents and the C quality was assessed by quantifying proportions of fast C (that is, rapidly released C) and active C (that is, potentially mineralizable C) in collected soil samples from each layer using long-term laboratory incubations (379 days) at a high temperature (29°C). In our sampling design, we ensured that permanent site conditions such as climate, soil type and texture, drainage, topography, and time since fire were independent of tree species composition, thus the variations of dependent variables are attributed to the effect of tree species composition and their associated understory vegetation.

Author's personal copy

Materials and Methods

Study Area

The study was conducted in two regions of the North American boreal forest in Canada. One study region was located in northwestern Ontario (named ''ON'' hereafter), approximately 150 km north of Thunder Bay (49°23′N to 49°37′N, 89°31′W to 89°45′W). The climate is boreal with a mean annual precipitation (MAP) totaling 712 mm and a mean annual temperature (MAT) of 2.5°C (Environment Canada 2010). Five stands dominated by jack pine, five stands dominated by trembling aspen, and five stands mixed uniformly with both tree species were selected for sampling in a 250 km^2 area with a maximum distance of 30 km between stands (total: 15 stands). The understory vegetation in the jack pine stands consisted of mainly the herbs *Cornus canadensis* L., *Maienthemum canadensis* Desf., *Linnea borealis* L., and feather-mosses, whereas the understory in the trembling aspen stands was dominated by the shrubs *Acer spicatum* Lamb., *Rubus pubescens* Raf., and *Ribes glandulosum* Grauer ex Weber and the herbs *M. canadensis*, *Mitella nuda* L., and *Aster macrophyllus* (L.) Cass. The understory in the mixedwood stands contained plant species found in both the jack pine and aspen stands. Soils were well-drained silty loam to sandy loam classified as Brunisols that originated from glacial till deposits (Soil Classification Working Group 1998). The topography was relatively flat and all stands originated from the same wildfire in 1923 (Senici and others 2010).

The second region was located in western Quebec (named ''QC'' hereafter), approximately 50 km northeast of La Sarre (49°08′N to 49°11′N, 78°46′W to 78°53′W). The climate is boreal with a MAP totaling 890 mm and a MAT of 0.7°C (Environment Canada 2010). Eight stands dominated by black spruce, eight stands dominated by trembling aspen, and eight stands mixed uniformly with both tree species were selected for sampling in a 100 km^2 area with a maximum distance of 10 km between stands (total: 24 stands). The understory vegetation in the black spruce stands consisted of mainly the herbs *C. canadensis*, *Rhododendron groenlandicum* (Oeder) Kron and Judd, *Vaccinium* spp., and big red stem moss (*Pleurozium schreberi* (Bird.) Mitt.); the latter was the dominant ground cover and an important input of organic matter to the soil (Bisbee and others 2001). In the aspen stands, by contrast, the understory was dominated by the shrubs *R. pubescens*, *Diervilla lonicera* Mill., and *Viburnum edule* (Michx.) Raf. and the herbs *C. canadensis*, *Viola* spp., *L. borealis*, and *M. canadensis*, whereas the mixedwood stands had an understory of plant species that were found in both the black spruce and aspen stands. Soils were moderately drained silty clay classified as Luvisols that originated from glaciolacustrine deposits (Soil Classification Working Group 1998). The topography was flat and all stands originated from the same wildfire in 1916 (Bergeron and others 2004).

Sampling

Similar to other studies that investigate tree species diversity effects in naturally established mature stands (for example, Wang and others 2002; Cavard and others 2010; Brassard and others 2011), the criteria for stand selection were that mixed-species stands would be relatively equal proportions of trembling aspen and jack pine (ON region) or black spruce (QC region) by stand basal area, whereas for single-species stands the basal area of a single tree species would be greater than 80% of the stand basal area (Table 1).

Table 1. Total Aboveground Litterfall in kg ha^{-1} y^{-1} (Mean ± SE) and Tree Species Composition (Mean % Tree Basal Area ± SE) of the Stand Types Located in Two Study Regions of the Canadian Boreal Biome

Stand properties	ON region			QC region		
	Jack pine	Mixedwood	Aspen	Black spruce	Mixedwood	Aspen
Litterfall	2272 ± 134	2574 ± 236	2651 ± 72	1853 ± 259	2756 ± 216	2467 ± 114
Species composition						
P. tremuloides	1.6 ± 1.5	35.5 ± 6.75	95.5 ± 1.11	1.5 ± 0.6	61.4 ± 4.1	88.9 ± 2.2
P. banksiana	83.3 ± 3.00	53.7 ± 7.09	0.7 ± 0.7	–	–	–
P. mariana	–	–	–	91.1 ± 3.4	33.5 ± 3.9	8.9 ± 1.7
Other species[1]	15.2 ± 2.13	10.8 ± 1.69	3.9 ± 0.8	7.4 ± 3.1	5.1 ± 1.5	2.2 ± 2.0

ON region, n = 5; QC region, n = 8.

[1] *Other species include jack pine and balsam fir (Abies balsamea (L.) Mill.) for the QC region and balsam fir, white spruce (Picea glauca (Moench) Voss), and white birch (Betula papyrifera Marsh.) for the ON region.*

Author's personal copy

To ensure that the variations of dependent variables are the result of tree species composition and their associated understory, we selected all stands in each respective region with the same permanent conditions: climate, soil type and texture, parent material, drainage, topography, and time since fire. Similarity of drainage class, parent material, and soil type was verified by digging a soil pit (ca. 1 m^3 in size) in each sampling plot (Soil Classification Working Group 1998). All selected stands were greater than 1 ha in area, fully stocked and visually homogeneous in structure and composition. 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 can be found in Brassard and others (2011), Cavard and others (2010), and Laganière and others (2011). We sought generality across the boreal biome by sampling two regions, but climatic and soil conditions differed among these regions. Consequently, our analysis was conducted separately for each region.

In each selected stand, a 400 m^2 circular plot was established to represent the stand. The species and diameter at breast height (DBH) of all trees larger than 5 cm DBH within each plot were determined and used for estimating tree species basal area for the assignment of stand type classification (Table 1). Total aboveground annual litterfall (that is, leaves, twigs, and other debris) was measured in each plot (kg ha^{-1} y^{-1}) using four 0.24 m^2 littertraps. Litterfall was collected from June 2006 to June 2008 in the ON region and from June 2007 to June 2008 in the QC region. Littertraps were emptied twice a year, and the collected litter was oven-dried at 50°C to a constant weight and weighed. Total aboveground annual litterfall was then calculated at each plot in the QC region by summing the oven-dried weights of collected litter from the two collection dates and scaling up to per ha. In the ON region, the oven-dried weights of collected litter from the four collection dates were summed and the resulting value was divided by two before being scaled up to per ha. The collected litter was not analyzed for litter quality parameters. However, data from Trofymow and others (1995) and Preston and others (2000) showed that black spruce and jack pine litters have a higher fraction of acid-unhydrolyzable residue (Klason lignin) and aromatic C regions and a lower fraction of water-soluble material compared with aspen litter. Moreover, higher proportions of nitrogen (N) and calcium were in the order jack pine > aspen > black spruce.

In June 2006, after complete soil thawing, four sampling points were randomly determined within each plot, where sampling points were at least 8 m apart. At each sampling point, a 15 × 15 cm^2 section of the entire organic layer (that is, forest floor or O horizon) was collected using a sharp knife and a trowel. One sample of the surface mineral layer (0–15 cm) was carefully extracted with a metal corer (diameter: 4.7 cm) directly beneath the collected organic layer. At two sampling points, a sample of the intermediate mineral layer (15–35 cm) was extracted, whereas at one sampling point a soil sample between 35 and 55 cm (deep mineral layer) was extracted.

Soil Analyses

All field-moist soil samples were passed through 6- and 4-mm sieves for organic and mineral layer samples, respectively. Soil bulk density was determined according to Maynard and Curran (2007). Subsamples were ground and analyzed for their C concentrations by dry combustion using a LECO CNS-2000 analyzer (Leco Corp., St. Joseph, MI, USA). As no carbonates were detected in any of the soil samples, C analysis was a measure of the total organic C concentration. C contents (in Mg C ha^{-1}) were then calculated by multiplying C concentrations with their respective soil bulk densities and sampling depths. Cation exchange capacity (CEC) was determined by summing exchangeable cations extracted with 0.1 M $BaCl_2$ and by atomic absorption spectrophotometry (Hendershot and others 2007). The pH was determined in water with a PHM82 pH meter (Radiometer, Copenhagen, Denmark) using a 1:2 soil:water ratio for mineral layers and a 1:10 ratio for organic layers. Soil texture was determined using the standard hydrometer method (Kroetsch and Wang 2007). All soil samples for bulk density and chemical properties were individually analyzed.

Microcosm Preparation

For the microcosm experiment, soil samples were pooled by depth for each circular plot to yield composite samples. Organic and mineral layer samples, 6- and 40-g dry weight, respectively, were placed on a layer of glass wool in 120-ml plastic containers (28 cm^2 surface area), wetted at field capacity, and placed in 500-ml glass jars (Mason type). These microcosms were left to equilibrate for 1 week at 2°C after handling and were then incubated in the laboratory at constant temperature (29°C) and soil moisture (field capacity) during 379 days. Long-term laboratory incubations followed by a modeling procedure is a useful empirical technique that provides an estimate of the

Author's personal copy

proportion of ''active C'' present in a soil sample under standard conditions (the remaining proportion of C being considered as stable or passive) by measuring the release of C by microbes over a long period of time (Paré and others 2006). The use of a high temperature allows the microbial community to mineralize a maximum of active organic material and increases the accuracy of the modeled active C values (modeling procedure) because the mineralization curves can reach a plateau earlier compared with incubations at low temperatures. A temperature between 20 and 35°C is commonly used to calculate active C (Zak and others 1993; Côté and others 2000; Halpern and others 2010; Maillard and others 2010).

Carbon Mineralization Measurements

Soil CO_2 efflux rates (C mineralization rates) were determined every week for the first 4 weeks and once a month thereafter (until the end of incubation). During measurements, the Mason jars were closed with airtight lids containing a rubber septum. The first gas sample was taken from the headspace with a syringe immediately after closing and directly injected into a LI-6200 infrared gas analyzer (LI-COR, St. Joseph, MI, USA) modified to allow us to measure a small volume of CO_2 (LI-COR, Application Note #121). The measurement was repeated after 16–48 h, depending on when an appropriate amount of CO_2 had accumulated in the Mason jars (depending on the soil layer and the progression of incubation).

Data Analysis

The mass of CO_2 emitted from each microcosm was calculated according to Paré and others (2006) and expressed as μg (C) per g of initial C mass per day. Cumulative amounts of C mineralized were calculated by adding the cumulative amount from the preceding period with the product of the average of daily mineralization rates of both periods by the number of days between both periods (Maillard and others 2010).

A first-order kinetic one-compartment exponential model was used to describe the cumulative C mineralization as a function of time:

$$\mathrm{C}_{\mathrm{cum}}(t) = \mathrm{C}_0 \times 1 - e^{-k_0 t}$$

where $\mathrm{C}_{\mathrm{cum}}(t)$ is the mean cumulative C mineralized at time t (mg C g^{-1} initial C), C_0 is the active C (mg C g^{-1} initial C), k_0 is the decomposition rate constant for mineralization of C (day^{-1}), and t is time (day). We used this model because it is more flexible than more complex models and is widely used to determine active C values. We fitted the C mineralization data of each individual soil sample to the model by means of a least square fitter (SigmaPlot v. 10.0, SYSTAT Software, Inc.) and calculated the proportion of active C at 29°C for each replicated sample.

To evaluate the proportion of fast C (that is, rapidly released C), indicative of high-quality organic matter (fast turnover), we used the value of the cumulative C mineralization after 3 months (100 days) of incubation at 29°C.

Statistical Analysis

Mean values (that is, fast, active, and total C proportions and contents) were compared between stand types and soil layers within each region using mixed linear models (PROC MIXED). Stand type and soil layer depth were considered as fixed effects whereas stand replicate was considered as a random effect. The following model was used:

$$Y_{ijk} = \mu + S_i + D_k + SD_{ik} + B_{j(i)} + \varepsilon_{ijk}$$

where Y_{ijk} is fast, active, or total C (proportions or contents), μ is the overall mean, S_i is stand type ($i = 1, 2, 3$), D_k is depth ($k = 1, 2, 3, 4$), SD_{ik} is the interaction between stand type and depth, $B_{j(i)}$ is stand replicates within stand type, and ε_{ijk} is the error. To better meet the assumptions of normality and homoscedasticity, the data were either log 10-transformed or square root-transformed. Differences between means were tested using orthogonal contrasts (CONTRAST statement). For presentation of our results, means and confidence limits were converted back to the original scale by reversing the transformation. Data were not compared statistically among regions for the reason mentioned earlier. The significance threshold was set at 0.05. Statistical analyses were performed using SAS v. 9.2 (SAS Institute, Cary, NC).

RESULTS

Amounts and Distribution of SOC

For both study regions, SOC stocks of the whole soil profile did not differ significantly among stand types (Figure 1; Table 2). The effect of stand type on total SOC contents, however, differed with soil depth (Figure 1; Table 2). In both regions, SOC contents generally decreased from the upper to the lower soil layers. In the ON region, C content of the organic layer was higher in the mixedwood than in the aspen stands (Figure 1A). In the surface (0–15 cm) and intermediate (15–35 cm) mineral

Author's personal copy

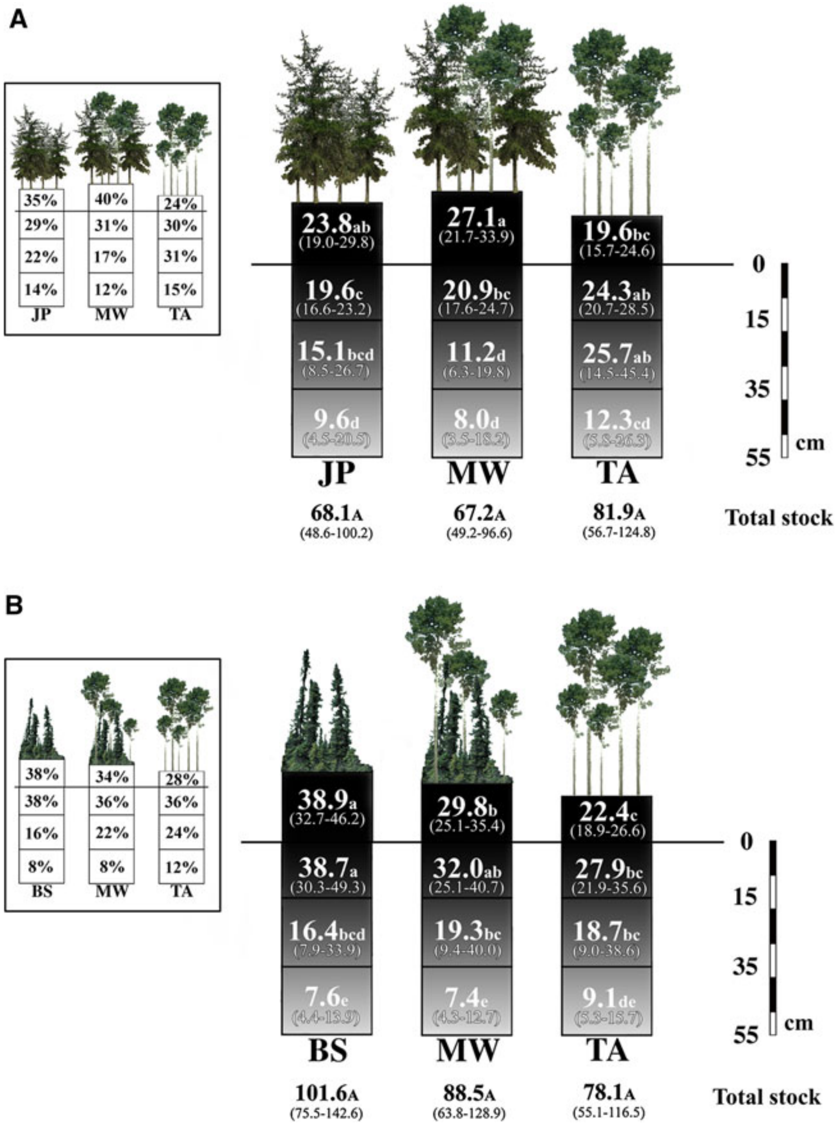

Figure 1. Amounts and distribution of SOC stocks (mg ha^{-1}) in different stand types located in the ON (**A**) and in the QC (**B**) regions of the Canadian boreal biome. *Different letters* across soil layer depths and stand types within a region represent a statistical difference between means according to mixed linear models as described in the "Materials and Methods" section. The relative SOC stock distribution (%) is shown on the upper left of each graph. Data are not compared across regions because climatic and soil conditions were not constant between ON and QC. 95% confidence limits are shown for each layer and total SOC stocks. *BS* black spruce, *JP* jack pine, *MW* mixedwood, *TA* trembling aspen. ON region, *n* = 5; QC region, *n* = 8.

Table 2. Effect of Stand Type, Soil Depth, and Interaction Term on Fast, Active, and Total C in Two Study Regions of the Canadian Boreal Biome

Effect	df	Contents						Proportions			
		Total C		Fast C		Active C		Fast C		Active C	
		F value	*P*	*F* value	*P*	*F* value	*P*	*F* value	*P*	*F* value	*P*
ON region											
Stand type (*S*)	2	0.10	0.909	1.87	0.203	0.27	0.772	2.49	0.097	1.46	0.246
Depth (*D*)	3	16.55	**<0.001**	81.48	**<0.001**	59.51	**<0.001**	56.80	**<0.001**	27.13	**<0.001**
S × *D*	6	2.48	**0.028**	1.80	0.134	2.73	**0.031**	0.55	0.764	1.73	0.142
QC region											
Stand type (*S*)	2	0.43	0.6543	1.81	0.188	3.30	**0.050**	10.15	**<0.001**	2.11	0.130
Depth (*D*)	3	40.85	**<0.001**	449.84	**<0.001**	125.39	**<0.001**	169.56	**<0.001**	30.92	**<0.001**
S × *D*	6	2.29	**0.036**	1.45	0.211	2.49	**0.034**	3.50	**0.004**	0.49	0.815

ON region, n = 5; QC region, n = 8. Bold indicates significant effects.

Author's personal copy

layers, C contents were higher in aspen stands than in jack pine and mixedwood stands, respectively, whereas no differences among stand types were detected in the deepest (35–55 cm) mineral layer. In the QC region, C contents of the organic layer and surface mineral layer were the highest in black spruce stands, followed by mixedwood and aspen stands, but C content did not differ among stand types for deeper soil layers (Figure 1B).

SOC Quality

The proportions of fast and active C varied significantly with soil layer depth (Table 2). Fast and active C proportions generally decreased with depth, and especially at the organic–mineral interface (Figures 2, 3). Differences in proportions of fast and active C among stand type were more pronounced in the organic layer. Specifically, in the ON region, less active C was found in aspen than in pine stands. In the QC region, a lower proportion of fast C was found in spruce than in aspen or mixedwood stands.

The contents of fast and active C varied significantly with soil layer depth (Table 2). In both regions, fast and active C contents decreased from the upper to the lower soil layers (Figure 4). Similar to total C, active C contents of the organic layer were the lowest in aspen stands of both regions (36–43% less), but this stand type effect diminished for all mineral layers (Figure 4A, B).

DISCUSSION

Similar to parent material, time, topography, and climate, biota plays a critical role in soil formation (Jenny 1994). Tree species composition in particular has been shown to have a strong influence on soil properties (for example, pH, C and nutrient contents, and soil community composition) and soil ecological processes (for example, decomposition and nutrient mineralization) (for example, Binkley 1995; Wardle and others 1997; Laganière and others 2009). However, tree species composition effects on soil attributes have been mostly observed in the organic layer (Wardle and others 1997; Alriksson and Eriksson 1998; Reich and others 2005; Hobbie and others 2006; Laganière and others 2009, 2010) and only rarely seen in the mineral soil (Finzi and others 1998; Giardina and others 2001; Vesterdal and others 2008). In this study, we found a significant difference in total SOC between stand types in the organic layer and surface mineral layer (0–15 cm) of both study regions, and in the intermediate (15–35 cm) mineral layer in the ON region. However, contrary to total SOC contents, the influence of stand type on SOC quality was restricted to the organic layer.

Although SOC stocks of the whole soil profile were not significantly different among stand types, probably owing to high variability and low sampling effort in deep horizons, the distribution of C across layers of the soil profile varied with forest composition. In the ON region, the greatest organic layer C stocks were found in mixed-species stands, whereas the lowest were found in aspen stands. The opposite was true for the mineral layer C stocks (the sum of all three mineral layers). In the QC region, the greatest amount of surface SOC (organic + surface mineral layer) was found in black spruce stands, followed by the mixedwood then by trembling aspen stands. SOC stocks below 15 cm were similar across stand types. Hence, the tendency for stands of tree species that favor low soil C contents near the surface to have more C in deeper soil layers, as highlighted by Vesterdal and others (2008), was only partly supported by our observations.

Organic Layer SOC

Stands containing coniferous species (single- and mixed-species) stored greater amounts of organic layer SOC than single-species aspen stands (Figure 1). The surface accumulation of SOC is mainly driven by rates of C input (litterfall and fine root mortality/turnover) and by C protection mechanisms such as the biochemical quality of litter and environmental constraints that affect rates of decomposition (Jandl and others 2007). Although annual tree litterfall in the aspen-dominated stands was greater than the jack pine- or black spruce-dominated stands (Table 1), the needle litter of conifers is often acidic, molecular-complex, and generally less palatable for soil decomposers compared with that of broadleaves (Aerts and Chapin 1999; Wardle 2002). In addition, the understory vegetation associated with coniferous stands (that is, bryophyte) is a major source of surface SOC that may surpass by several times the amount of tree-originated C returned to the soil (Oechel and Van Cleve 1986). Bryophytes also favor cold and wet field conditions and, in general, they decompose slowly (Légaré and others 2005; Gornall and others 2007; Lang and others 2009). This was supported by the fact that we observed the lowest proportion of fast C found in the organic layer of the black spruce stands, indicating a slow C turnover even under optimal laboratory conditions (Figure 3B). Therefore, accumulation of surface SOC would be favored in

Author's personal copy

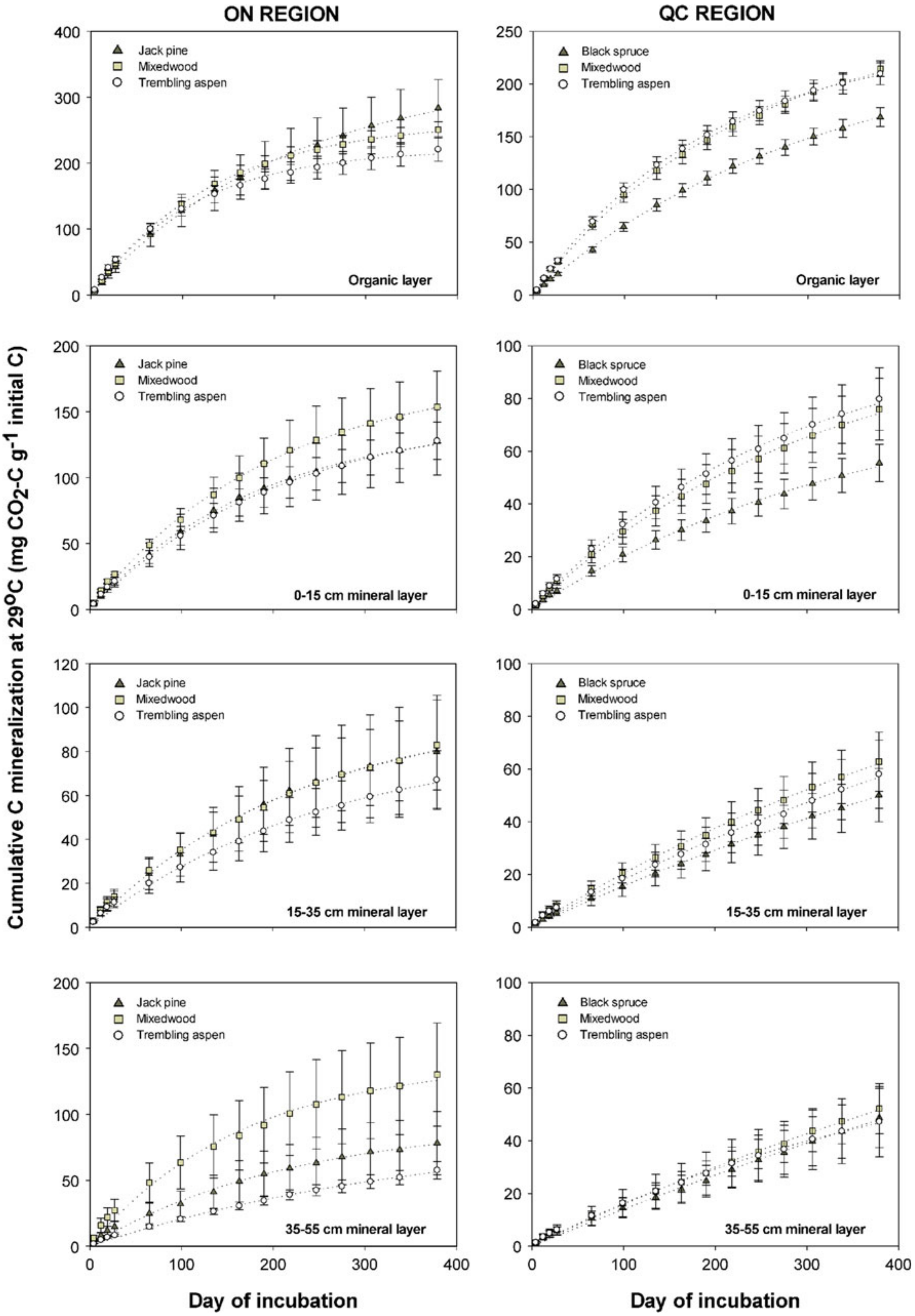

Figure 2. Cumulative C mineralized within layers of the soil profile in different stand types located in two regions of the Canadian boreal biome during 379 days of incubation at 29°C. Scale of *y*-axis is not constant among soil layers and regions. *Error bars* are ±SE. ON region, $n = 5$; QC region, $n = 8$.

Author's personal copy

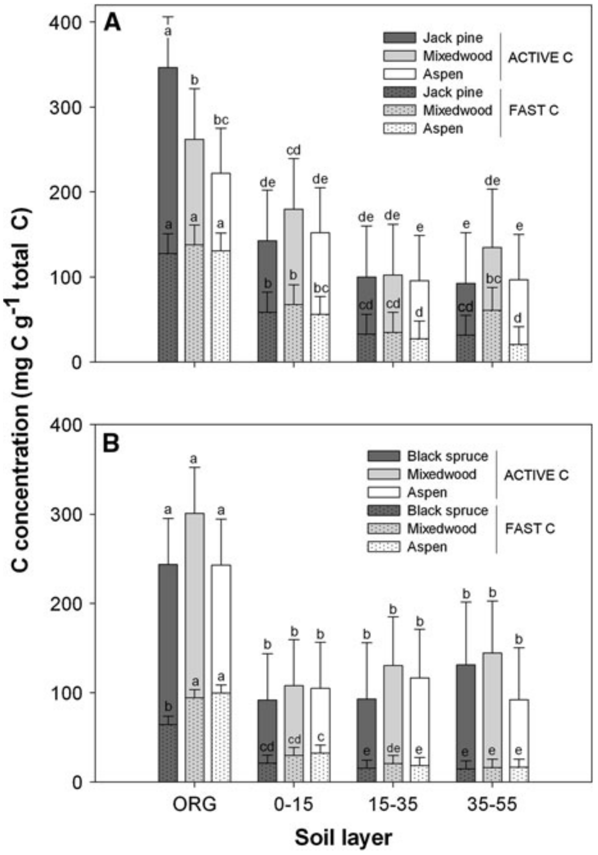

Figure 3. Proportions of fast and active C contained in SOC stocks within layers of the soil profile in different stand types located in the ON (**A**) and in the QC (**B**) regions of the Canadian boreal biome. *Different letters* represent a statistical difference between means at $P < 0.05$ according to mixed linear models as described in the "Materials and Methods" section. *Error bars* are 95% upper confidence limits. ON region, $n = 5$; QC region, $n = 8$.

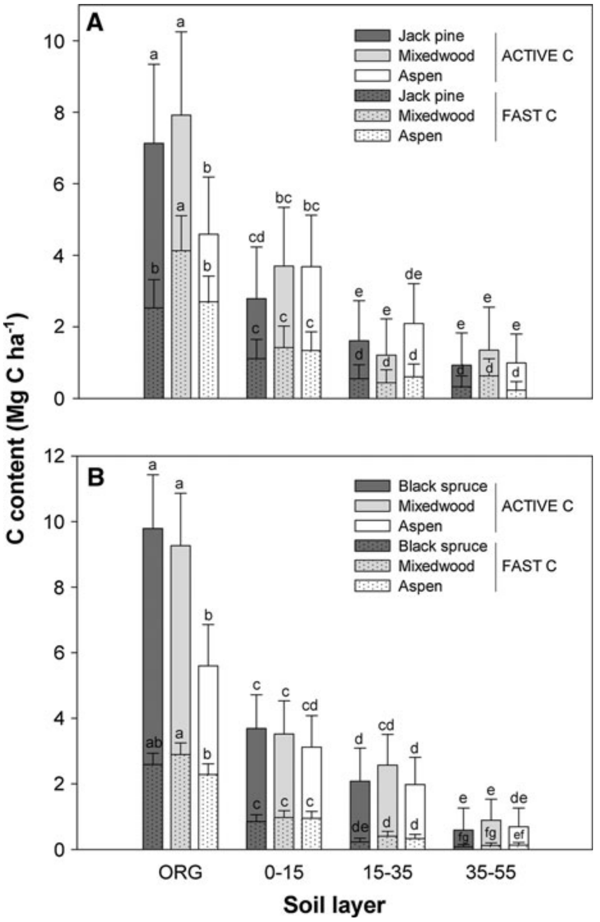

Figure 4. Amounts of fast and active C contained within layers of the soil profile in different stand types located in the ON (**A**) and in the QC (**B**) regions of the Canadian boreal biome. Scale of *y*-axis is not constant among regions. *Different letters* represent a statistical difference between means at $P < 0.05$ according to mixed linear models as described in the "Materials and Methods" section. *Error bars* are 95% upper confidence limits. ON region, $n = 5$; QC region, $n = 8$.

coniferous stands because C output rates are generally low, as micro-environmental conditions and the nature of C inputs promote slow litter decomposition. In support of this, Laganière and others (2012) found annual C losses through heterotrophic respiration to be lower in black spruce than in aspen stands due to colder soil in addition to other factors driving the accumulation and quality of C.

In the ON region, by contrast, the greatest amount of organic layer C occurred in the mixedwood stands and not the pure coniferous stands, that is, jack pine (Figure 1A). Similarly, Brassard and others (2011) for the same study area found mixed-species stands to have higher fine root productivity than single-species stands; whereas, Cavard and others (2010) found no relationship between tree species diversity and aboveground tree productivity. Greater C accumulation in the organic layer thus correlates with the belowground component but not with the aboveground one. Facilitation, niche partitioning, and greater stability (resistance) to disturbances have been suggested to explain why certain mixed-species stands can support greater biomass production relative to their single-species counterparts (Jandl and others 2007; Lorenz and Lal 2010). Along with a low proportion of active C (Figure 3A), the possible occurrence of these mechanisms may explain the synergistic response of organic layer SOC storage to the aspen-jack pine mixture.

A large proportion of the C found in the organic layer of both regions was active SOC. The size of the active C pool ranged from 16% to as high as 49% of SOC, with an average of 27% and a standard deviation of 8% (data not shown). Likewise,

Author's personal copy

Neff and Hooper (2002) estimated that potentially mineralizable C in the soils of northern latitudes may be between 9 and 41%. Although nearly three quarters of organic layer SOC may be qualified as stable in our study, the active SOC pool of the boreal biome is considerable in absolute numbers, and is substantially greater than that found in other biomes (temperate and tropical), where the active pool generally represents only 2–3% and is far less important on an absolute basis (Neff and Hooper 2002; Fissore and others 2009). Consequently, the response of decomposition to warming could be less constrained by C availability in boreal than in temperate or tropical soils (Neff and Hooper 2002).

Because the proportions of active C varied among stand types (Figure 3), the stability of organic layer SOC stocks appears to differ with forest composition in the boreal biome. Given that less active C was generally found in aspen stands, the organic layer SOC in aspen stands is more stable compared with SOC in the organic layer of the other stand types we studied (Figure 4). Greater N availability in the late stages of the decomposition process has been suggested to increase organic matter stabilization and reduce the decomposition limit value, that is, the point when decay virtually ceases (Berg and others 1996, 2001). A higher organic layer N concentration in trembling aspen compared with the other stand types (Appendix A) might thus explain the lower content of C potentially available for microbes to mineralize, that is, active SOC, in the aspen stands.

Mineral Layer SOC

Accumulation of SOC in mineral layers is more complex than in the organic layer. It depends on both the aboveground and belowground C sources (for example, dissolved organic C from the organic layer, root turnover, and rhizodeposition), and involves important stabilization mechanisms that include chemical and physical protection within soil aggregates (Rumpel and Kögel-Knabner 2011), which confer to the C, and especially that in deep layers, a mean residence time on the order of millennia (Jenkinson and others 2008). Probably due to these differences in C sources, in the organo-mineral interactions and in the degree of microbial processing, we found a decrease in cumulative C mineralization and in fast and active C proportions from the organic to the mineral layers (Figures 2, 3). Accumulation of SOC in the mineral soil may also depend on the characteristics of the organic layer lying above it. Indeed, in boreal ecosystems and especially in conifer stands such as in black spruce stands, a thick organic layer with insulating properties can develop and influence the thermal regime of the mineral soil underneath by reducing air–soil heat transfers during the growing season (Carrasco and others 2006). A colder soil would thus slow microbial activity and favor C accumulation in surface mineral layers.

In a previous experiment aiming to evaluate the influence of forest composition on soil aggregation and soil size-density fractions in the surface mineral layer of the QC sites, Laganière and others (2011) showed that contents of the less-protected fractions (that is, uncomplexed organic matter), commonly considered as the active pool of SOC, corresponded to 16.0, 11.3, and 7.7 Mg C ha^{-1} in black spruce, mixedwood, and aspen stands, respectively. By comparison, we found that biologically active SOC pools were 3.8, 3.7, and 3.4 Mg C ha^{-1} in black spruce, mixedwood, and trembling aspen, respectively (Figure 4B). The higher reported values of Laganière and others (2011) compared with this study for the same stands may be the result of uncomplexed organic matter containing not only active SOC but also biochemically resistant SOC and a variable proportion of particulate organic matter that is physically protected within macroaggregates and not readily available to microbes (Gregorich and others 2006; von Lützow and others 2007).

Across the soil profile, SOC located in deep layers should be more stable than surface SOC for several reasons including the fact that deep SOC is usually more processed and thus has a lower quality than surface SOC, as indicated by the lower proportion of fast C below a depth of 15 cm (Figure 3) and the lower C:N ratios (Appendix A). Deep SOC is also considered stable because low temperatures and a high heterogeneity of C input limit microbial activity at deep soil depths (Salomé and others 2010; Rumpel and Kögel-Knabner 2011), because deep SOC is protected against combustion during wildfire (Neff and others 2005) and because decomposition of deep SOC is limited by fresh C supply (Fontaine and others 2007). Moreover, deep-rooting tree species may accumulate more C in deep soil layers, whereas stands of shallow-rooting species may accumulate more C in the upper layers (Lorenz and Lal 2010). Although the roots of aspen and jack pine can reach a depth of 100 cm, black spruce roots rarely exceed 30 cm in depth and most of the roots are located at the organic–mineral interface (Strong and La Roi 1983). These specific root patterns apparently coincide with our SOC accumulation patterns. Only 25% of the total SOC stock in black spruce stands was located below a depth of 15 cm,

Author's personal copy

compared with 36% for jack pine stands and 36% and 46% for trembling aspen stands in the QC and the ON regions, respectively (30% for both mixedwoods) (Figure 1). Consequently, the SOC stock in the trembling aspen stands could be regarded as more stable because a larger part of the SOC is distributed in deep soil layers, where organic matter quality is lower and conditions for microbial activity are harsher relative to the other stand types.

Mechanisms Behind Forest Composition Effect on SOC Stocks and Implications for Global Changes: Black Spruce Versus Trembling Aspen

Figure 5 represents a conceptual scheme depicting the mechanisms that explain tree species composition effects on the size and stability of SOC stocks using the two most distinct stand types in this study and the ones with the more information we have on so far, that is, black spruce versus aspen stand in the QC region. It is proposed that compared with aspen, black spruce soils store more SOC but that this C would be more prone to loss under a changing environment, mainly because of weak SOC stabilization and important tree species-induced microclimatic constraints to decomposition. Indeed, the micro-environmental conditions generated under black spruce favor the development of a thick moss carpet that contributes to keeping the soil cold and wet (Légaré and others 2005; Gornall and others 2007; Lang and others 2009; Laganière and others 2012). Along with spruce needles that are acidic and of low palatability for macro-invertebrate shredders (Vance and Chapin 2001; Laganière and others 2010), mosses, representing a large C input to the soil in black spruce forests, are slow to decompose (Lang and others 2009). The activity of phenol oxidase, which is responsible for phenolic materials degradation such as lignin, is limited in cold, wet, and acidic environments with a low oxygen status (Sinsabaugh 2010).

In addition, the thicker organic layer in black spruce stands cools the mineral soil underneath and thus reduces decomposition rates. For all these reasons, black spruce soils are characterized by a slow C turnover and organic matter can thus accumulate in the organic and surface mineral layers, as shown in this study. Although SOC accumulation is greater in black spruce than in aspen soils, SOC stabilization is weak in black spruce soils. Indeed, Laganière and others (2011) found that the extra SOC stored in the surface

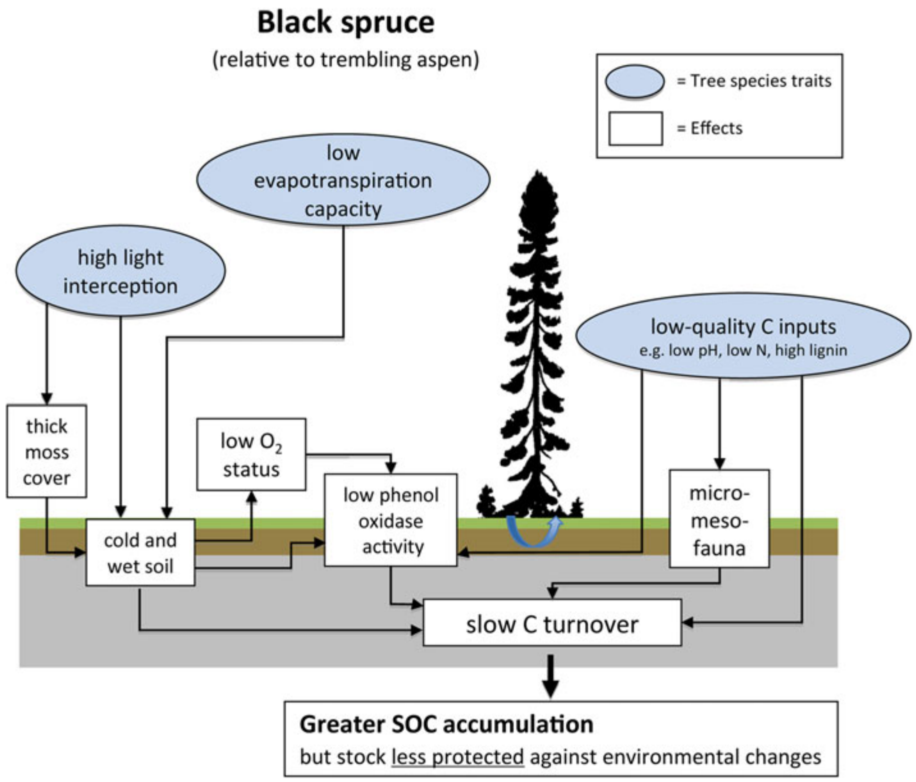

Figure 5. Conceptual scheme depicting the mechanisms that explain tree species composition effects on the size and stability of SOC stocks developed in black spruce stands relative to that developed in aspen stands in the QC region.

Author's personal copy

mineral layer under black spruce was in fact labile and less mineral-protected relative to aspen. In addition, in a field respiration study in the same study area, decomposition of soil organic matter produced in black spruce stands was more temperature-sensitive than that in aspen stands (Q_{10} = 2.7 ± 0.2 vs. 2.0 ± 0.2) (Laganière and others 2012). Therefore, because decomposition of the accumulated labile organic matter is in part limited by environmental constraints (tree species-induced micro-climatic effects) and that temperature sensitivity of decomposition is greater in black spruce stands relative to aspen, any changes in micro-climatic conditions that would enhance soil microbial activity and especially an increase in soil temperature (induced by climate change or by a natural/human disturbance) could release this accumulated organic matter. This finding is of particular concern for the forest C budget because black spruce largely dominates the boreal landscape in Canada.

CONCLUSION

We showed that distribution and quality of SOC differed among stand types in the Canadian boreal forest. In general, SOC in the trembling aspen stand was the most stable, as exemplified by larger amounts of deep SOC and a lower proportion of active C in the organic layer. Despite less litterfall, black spruce stands allowed a greater accumulation of SOC in surface layers because of low-quality C inputs and soil microclimatic conditions limiting decomposition. These stocks, however, might become vulnerable to extra losses if soil conditions become more favorable to decomposition under climate change. Our analysis highlights that boreal forest composition could have implications for stability of SOC stocks and incidentally how climate change could alter this large C pool.

ACKNOWLEDGMENTS

This study was funded through the Natural Sciences and Engineering Research Council of Canada (SPG281886) and the Fonds Québécois de la Recherche sur la Nature et les Technologies. We acknowledge the support from Produits Forestiers Résolu, Tembec, BIOCAP Canada, the Ontario Ministry of Natural Resources, and the Canadian Forest Service. We are grateful to Luc St-Antoine, Éric Girard, Jessie Parent, Stephen Hart, and Alain Courcelles for their valuable assistance in the field and in the laboratory. We thank Michèle Bernier-Cardou for her statistical assistance and Yan Boulanger for comments on an earlier version of the manuscript.

REFERENCES

Aerts R, Chapin FS. 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67.

Alriksson A, Eriksson HM. 1998. Variations in mineral nutrient and C distribution in the soil and vegetation compartments of five temperate tree species in NE Sweden. For Ecol Manag 108:261–73.

Berg B. 2000. Litter decomposition and organic matter turnover in northern forest soils. For Ecol Manag 133:13–22.

Berg B, Johansson M-B, Ekbohm G, McClaugherty C, Rutigliano F, Santo AVD. 1996. Maximum decomposition limits of forest litter types: a synthesis. Can J Bot 74:659–72.

Berg B, McClaugherty C, De Santo AV, Johnson D. 2001. Humus buildup in boreal forests: effects of litter fall and its N concentration. Can J For Res 31:988–98.

Bergeron Y, Gauthier S, Flannigan M, Kafka V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85:1916–32.

Binkley D. 1995. The influence of tree species on forest soils: processes and patterns. In: Mead DJ, Cornforth IS, Eds. Proceedings of the trees and soils workshop. Special Publication No. 10. Canterbury: Agronomy Society of New Zealand. pp 1–33.

Bisbee KE, Gower ST, Norman JM, Nordheim EV. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia 129:261–70.

Bond-Lamberty B, Peckham SD, Ahl DE, Gower ST. 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450:89–92.

Bossuyt H, Six J, Hendrix PF. 2005. Protection of soil carbon by microaggregates within earthworm casts. Soil Biol Biochem 37:251–8.

Brassard BW, Chen HYH, Bergeron Y, Paré D. 2011. Differences in fine root productivity between mixed- and single-species stands. Funct Ecol 25:238–46.

Brassard B, Chen HYH, Cavard X, Laganière J, Reich PB, Bergeron Y, Paré D, Yuan Z. 2013. Tree species diversity increases fine root productivity through increased soil volume filling. J Ecol 101:210–19.

Canada's NFI. 2010. Canada's National Forest Inventory: monitoring the sustainability of Canada's Forests. Ottawa, ON: Canadian Council of Forest Ministers. http://nfi.nfis.org.

Carrasco JJ, Neff JC, Harden JW. 2006. Modeling physical and biogeochemical controls over carbon accumulation in a boreal forest soil. J Geophys Res 111:G02004.

Cavard X, Bergeron Y, Chen HYH, Paré D. 2010. Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. Can J For Res 40:37–47.

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.

De Deyn GB, Cornelissen JHC, Bardgett RD. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol Lett 11:516–31.

Environment Canada. 2010. Canadian climate normals or averages 1971–2000. Fredericton, NB: Environment Canada. http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html.

Author's personal copy

Finzi AC, Van Breemen N, Canham CD. 1998. Canopy tree–soil interactions within temperate forests: species effects on soil carbon and nitrogen. Ecol Appl 8:440–6.

Fissore C, Giardina CP, Swanston CW, King GM, Kolka RK. 2009. Variable temperature sensitivity of soil organic carbon in North American forests. Glob Chang Biol 15:2295–310.

Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–81.

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.

Gornall JL, Jónsdóttir IS, Woodin SJ, Van der Wal R. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153:931–41.

Gower ST, Hunter A, Campbell J, Vogel J, Veldhuis H, Harden J, Trumbore S, Norman JM, Kucharik CJ. 2000. Nutrient dynamics of the southern and northern BOREAS boreal forests. Ecoscience 7:481–90.

Gregorich EG, Beare MH, McKim UF, Skjemstad JO. 2006. Chemical and biological characteristics of physically uncomplexed organic matter. Soil Sci Soc Am J 70:975–85.

Halpern MT, Whalen JK, Madramootoo CA. 2010. Long-term tillage and residue management influences soil carbon and nitrogen dynamics. Soil Sci Soc Am J 74:1211–7.

Hart SA, Chen HYH. 2006. Understory vegetation dynamics of North American boreal forests. Crit Rev Plant Sci 25:381–97.

Hendershot WH, Lalande H, Duquette M. 2007. Ion exchange and exchangeable cations. In: Carter MR, Gregorich EG, Eds. Soil sampling and methods of analysis. 2nd edn. Boca Raton, FL: CRC Press. p 197–206.

Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karolewski P. 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87:2288–97.

Ilisson T, Chen HYH. 2009. Response of six boreal tree species to stand replacing fire and clearcutting. Ecosystems 12:820–9.

IPCC. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge, UK: Cambridge University Press.

Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA. 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137:253–68.

Jenkinson DS, Poulton PR, Bryant C. 2008. The turnover of organic carbon in subsoils. Part 1. Natural and bomb radiocarbon in soil profiles from the Rothamsted long-term field experiments. Eur J Soil Sci 59:391–9.

Jenny H. 1994. Factors of soil formation. A system of quantitative pedology. New York, NY: Dover Publications.

Jobbagy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10:423–36.

Kroetsch D, Wang C. 2007. Particle size distribution. In: Carter MR, Gregorich EG, Eds. Soil sampling and methods of analysis. 2nd edn. Boca Raton, FL: CRC Press. p 713–26.

Laganière J, Paré D, Bradley RL. 2009. Linking the abundance of aspen with soil faunal communities and rates of belowground processes within single stands of mixed aspen-black spruce. Appl Soil Ecol 41:19–28.

Laganière J, Paré D, Bradley RL. 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Can J For Res 40:465–75.

Laganière J, Angers DA, Paré D, Bergeron Y, Chen HYH. 2011. Black spruce soils accumulate more uncomplexed organic matter than aspen soils. Soil Sci Soc Am J 75:1125–32.

Laganière J, Paré D, Bergeron Y, Chen HYH. 2012. The effect of boreal forest composition on soil respiration is mediated through variations in soil temperature and C quality. Soil Biol Biochem 53:18–27.

Lang SI, Cornelissen JHC, Klahn T, van Logtestijn RSP, Broekman R, Schweikert W, Aerts R. 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. J Ecol 97:886–900.

Légaré S, Paré D, Bergeron Y. 2005. Influence of aspen on forest floor properties in black spruce-dominated stands. Plant Soil 275:207–20.

Lorenz K, Lal R. 2010. Carbon sequestration in forest ecosystems. Dordrecht, The Netherlands: Springer.

Maillard E, Paré D, Munson AD. 2010. Soil carbon stocks and carbon stability in a twenty-year-old temperate plantation. Soil Sci Soc Am J 74:1775–85.

Maynard DG, Curran MP. 2007. Bulk density measurement in forest soils. In: Carter MR, Gregorich EG, Eds. Soil sampling and methods of analysis. 2nd edn. Boca Raton, FL: CRC Press. p 863–9.

Neff JC, Hooper DU. 2002. Vegetation and climate controls on potential CO_2, DOC and DON production in northern latitude soils. Glob Chang Biol 8:872–84.

Neff JC, Harden JW, Gleixner G. 2005. Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. Can J For Res 35:2178–87.

Oechel WC, Van Cleve K. 1986. The role of bryophytes in nutrient cycling in the Taiga. In: Van Cleve K, Chapin FS III, Flanagan PW, Viereck LA, Dyrness CT, Eds. Forest ecosystems in the Alaskan taiga. Berlin, Germany: Springer. p 121–37.

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.

Preston CM, Trofymow JA, Canadian Intersite Decomposition Experiment Working Group. 2000. Variability in litter quality and its relationship to litter decay in Canadian forests. Can J Bot 78:1269–87.

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG. 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol Lett 8:811–18.

Rumpel C, Kögel-Knabner I. 2011. Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. Plant Soil 338:143–58.

Salomé C, Nunan N, Pouteau V, Lerch TZ, Chenu C. 2010. Carbon dynamics in topsoil and in subsoil may be controlled by different regulatory mechanisms. Glob Chang Biol 16:416–26.

Senici D, Chen HYH, Bergeron Y, Cyr D. 2010. Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems 13:1227–38.

Sinsabaugh RL. 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. Soil Biol Biochem 42:391–404.

Author's personal copy

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd edn. Ottawa, ON: Agriculture and Agri-Food Canada, Research Branch, Publication No. 1646.

Soja AJ, Tchebakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Parfenova EI, Chapin FS III, Stackhouse PW Jr. 2007. Climate-induced boreal forest change: predictions versus current observations. Global Planet Change 56:274–96.

Strong WL, La Roi GH. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Can J For Res 13:1164–73.

Trofymow JA, Preston CM, Prescott CE. 1995. Litter quality and its potential effect on decay rates of materials from Canadian forests. Water Air Soil Pollut 82:215–26.

Vance ED, Chapin FS. 2001. Substrate limitations to microbial activity in taiga forest floors. Soil Biol Biochem 33:173–88.

Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P. 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For Ecol Manag 255:35–48.

von Lützow M, Kögel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner B, Flessa H. 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions—a review. Eur J Soil Sci 57:426–45.

von Lützow M, Kögel-Knabner I, Ekschmitt K, Flessa H, Guggenberger G, Matzner E, Marschner B. 2007. SOM fractionation methods: relevance to functional pools and to stabilization mechanisms. Soil Biol Biochem 39:2183–207.

Wang XL, Klinka K, Chen HYH, de Montigny L. 2002. Root structure of western hemlock and western redcedar in single- and mixed-species stands. Can J For Res 32:997–1004.

Wardle DA. 2002. Communities and ecosystems: linking the aboveground and belowground components. Princeton, NJ: Princeton University Press.

Wardle DA, Zackrisson O, Hörnberg G, Gallet C. 1997. The influence of island area on ecosystem properties. Science 277:1296–9.

Zak DR, Grigal DF, Ohmann LF. 1993. Kinetics of microbial respiration and nitrogen mineralization in Great Lakes forests. Soil Sci Soc Am J 57:1100–6.