Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests

Xavier Cavard, Yves Bergeron, Han Y.H. Chen, and David Paré

Abstract: This study investigates the potential of mixed forest stands as better aboveground carbon sinks than pure stands. According to the facilitation and niche complementarity hypotheses, we predict higher carbon sequestration in mature boreal mixedwoods. Aboveground carbon contents of black spruce (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.) and trembling aspen (*Populus tremuloides* Michx.) mixtures were investigated in the eastern boreal forest, whereas jack pine (*Pinus banksiana* Lamb.) and trembling aspen were used in the central boreal forest. No carbon gain was found in species mixtures; nearly pure trembling aspen stands contained the greatest amount of aboveground carbon, black spruce stands had the least, and mixtures were intermediate with amounts that could generally be predicted by linear interpolation with stem proportions. These results suggest that for aspen, the potentially detrimental effect of spruce on soils observed in other studies may be offset by greater light availability in mixtures. On the other hand, for black spruce, the potentially beneficial effects of aspen on soils could be offset by greater competition by aspen for nutrients and light. The mixture of jack pine and trembling aspen did not benefit any of these species while inducing a loss in trembling aspen carbon at the stand level.

Résumé : Cette étude vise à déterminer si les peuplements forestiers mixtes peuvent être des puits de carbone aériens plus efficaces que les peuplements purs. En accord avec les hypothèses de facilitation et de séparation des niches écologiques, nous prédisons une plus grande séquestration du carbone dans les peuplements mixtes. Nous avons donc déterminé les stocks de carbone aériens dans des mélanges d'épinettes noires (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.) et de peupliers faux-tremble (*Populus tremuloides* Michx.) situés dans la forêt boréale de l'est, tandis que des mélanges de pin gris (*Pinus banksiana* Lamb.) et de peupliers faux-tremble furent plutôt utilisés dans la forêt boréale centrale. Les mélanges d'espèces ne présentaient aucun gain en carbone. Les peuplements dominés par le tremble contenaient la plus grande quantité de carbone aérien, les pessières la plus petite quantité, et les mélanges en contenaient des quantités intermédiaires qui pouvaient généralement être prédites par interpolation linéaire en fonction de la proportion de tiges de chaque espèce. Ces résultats suggèrent que dans le cas du tremble, l'effet potentiellement néfaste de l'épinette sur les sols peut être compensé par une meilleure disponibilité de la lumière dans les peuplements mixtes. Parallèlement, dans le cas de l'épinette noire, l'effet potentiellement bénéfique du peuplier faux-tremble sur les sols pourrait être contrebalancé par une compétition accrue pour la lumière et les nutriments en sa présence. Le mélange de pin gris et de peuplier faux-tremble n'a apporté aucun bénéfice pour aucune des deux espèces tout en induisant une perte en carbone chez le tremble à l'échelle du peuplement.

Introduction

With the increasing attention given to the problem of global climate change, many researchers have focused on vegetation carbon sequestration as part of a possible solution (IPCC 2007). The emphasis has been put on forest ecosystems, which contain nearly 77% of vegetation carbon and 42% of soil carbon in the world (Bolin and Sukumar 2000). Although the main concern is about deforestation in tropical regions, the boreal forest, which contains about 30% of the Earth's phytomass (Bailey 1996), is an important sink in global carbon balance (Goodale et al. 2002).

Mixedwoods represent one-half of the Canadian boreal forest (CCFM 2000). Although they are globally disregarded in forest management, mixedwoods may have many advantages over pure stands, including higher productivity (Man and Lieffers 1999; Johansson 2003; MacDonald and Thompson 2003; Pretzsch 2003), which can translate into higher carbon sequestration. Thus, mixedwoods could contribute to increasing the carbon sink capacity of boreal forests. However, the mixture effect on productivity is controversial. Two mechanisms potentially inducing higher productivity in mixedwoods were proposed by Vandermeer (1989): (*i*) facilitation, i.e., a species promoting the growth or survival of another, mostly by improving abiotic conditions; and (*ii*) niche complementarity, i.e., a better and less competitive use of ecosystem resources between species having distinct functional traits (e.g., a shade-tolerant species growing under an intolerant one). A commonly studied facilitation effect is a higher rate of litter decomposition

Received 30 March 2009. Resubmitted 30 July 2009. Accepted 29 September 2009. Published on the NRC Research Press Web site at cjfr.nrc.ca on 27 January 2010.

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and, thus, of nutrient cycling that could be induced by tree mixtures, particularly the admixture of a broadleaf species with a coniferous one (Côté et al. 2000; Prescott et al. 2000). The mixture effect on nutrition and litter decomposition proved largely dependent on the particular species used in the mixture and of the initial soil conditions (Rothe and Binkley 2001; Rothe et al. 2002; Gartner and Cardon 2004; Godefroid et al. 2005). Similarly, the mixture effect on productivity can be positive, negative, or null depending on the species considered (Brown 1992; Kelty 1992; Chen and Klinka 2003; Lindén and Agestam 2003). Nonoverlapping of the functional traits of species could be a factor that determines the outcome of the mixture effect, especially shade tolerance or intolerance (Chen et al. 2003). The mixture effect also depends on the environmental conditions, which can alter it even when the same species are used (Wang and Kimmins 2002; Green and Hawkins 2005).

This study investigating the mixture effect is part of a broader project in which all major carbon pools and fluxes will be estimated in the same stands, but this paper will focus on the carbon pool that is the most dynamic during a forest rotation, that of the living trees. Because the mixture effect can potentially differ depending on component species and abiotic conditions, two kinds of mixtures were studied: (*i*) mature black spruce (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.) and trembling aspen (*Populus tremuloides* Michx.) mixedwoods and their respective single-species stands in the Clay Belt of northwestern Quebec, and (*ii*) mature jack pine (*Pinus banksiana* Lamb.), trembling aspen, and black spruce mixedwoods and respective pure stands on till deposits in northwestern Ontario. We hypothesized that (*i*) given the potential positive effect of trembling aspen on soil quality (Côté et al. 2000; Prescott et al. 2000; Fenton et al. 2005; Légaré et al. 2005*b*) and the low shade cast by this shade-intolerant species (Canham et al. 1994; Messier et al. 1998), aspen's presence should have a positive effect on black spruce individual carbon content in mixedwoods; (*ii*) on the other hand, black spruce is always overtopped by trembling aspen. Therefore, there is an anticipated increase in light availabilty for aspen when competing with black spruce but the adverse effect of black spruce on soil quality (Prescott et al. 2000; Crawford et al. 2003) could have a negative impact on aspen. Thus, the balance between these two effects could induce a null effect of black spruce on trembling aspen carbon content in mixedwoods, and (*iii*) because trembling aspen and jack pine have similar growth patterns (Longpré et al. 1994) with the latter being not very responsive to differences in soil fertility (Béland and Bergeron 1996), no mixture effect should be observed in aspen–pine mixedwoods. Meanwhile, black spruce could benefit from the higher soil quality induced by aspen and, thus, sequester more carbon under aspen than under jack pine.

Materials and methods

Study areas

This study took place in two distinct areas of the boreal mixedwood forest region. The first was located in the black spruce – feathermoss forest of western Quebec (Bergeron 1996), at the border of the Abitibi-Témiscamingue and Nord-du-Québec regions (49°08′N to 49°11′N, 78°46′W to 78°53′W). This area is part of the Clay Belt region of Quebec and Ontario. This major physiographic region results from deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse during the Wisconsinian glacial stage (Veillette 1994). The closest meteorological station is located in La Sarre (ca. 30 km south). Mean annual temperature is 0.7 °C, and mean annual precipitation totals 889.8 mm (Environment Canada 2007). All study sites were located on subhygric Grey Luvisols (Soil Classification Working Group 1996).

The second study area was located approximately 100 km north of Thunder Bay in northwestern Ontario (49°23′N to 49°36′N, 89°31′W to 89°44′W). Mean annual temperature and mean total annual precipitation have been estimated at 0.9 °C and 712.8 mm, respectively, by the BIOSIM model from 1977 to 2006 climatic data (Régnière and St-Amant 2007). The study was conducted on mesic upland sites whose soils are relatively deep glacial tills belonging to the Brunisolic order (Soil Classification Working Group 1996). Jack pine, trembling aspen, black spruce, and white birch (*Betula papyrifera* Marsh.) occur in this area in mixed dominance with white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.).

Sampling design

Quebec study

Twenty-four sampling plots (see Table 1 for plot characteristics) were established across eight blocks, located in the same 36 km^2 area (maximum distance between blocks: 7 km), dominated by black spruce with patches of aspen. All these stands originated from a fire that occurred in 1916 (Légaré et al. 2005*a*). Within each block (numbered from I to VIII), three plots of distinct compositions were selected: pure black spruce, pure trembling aspen, and mixedwoods containing both species (hereafter named BS, TA, and MW, respectively). After measurements, one plot (VIII-BS) proved unsuitable and, therefore, was discarded from all analyses.

In our study, pure stands contained >75% of the dominant species in relative basal area, whereas mixedwoods were selected so as to have <75% of one species in relative basal area, with stems of different species evenly spread across the stand (''intimate'' mixture). All three plots of a given block were separated by 40–100 m to minimize the variability within each block (complete random block design). We made sure the species proportions were different enough among plots belonging to a same block.

Ontario study

Six composition types were used in the Ontario study (Table 1): pure jack pine (JP), pure aspen (TA), pine–aspen mixedwoods (MW) with the same selection criteria as those in the Quebec study and the same three overstory types with a black spruce subcanopy of ≥15% of plot total basal area (denoted JPbs, TAbs, MWbs, respectively). Each composition type was replicated between two and five times. The study plots were established across an area of approximately 250 km^2. All plots originated from fire, with mean breast height age ranging from 59 to 74 years old for pine and as-

Table 1. Overstory characteristics of the study plots.

	Basal area (%)*				Breast height age (years)*				
Area and composition†	Black spruce	Trembling aspen	Jack pine	Other species‡	Black spruce	Trembling aspen	Jack pine	Total density (stems·ha^{-1})*,§	No. of replicates
Quebec									
BS	89.4±4.2	1.8±0.7	—	8.8±4.0	69.5±0.9	—	—	3115±380	7
MW	33.8±3.6	59.5±3.5	—	6.7±1.6	72.0±0.8	75.8±1.1	—	1578±125	8
TA	8.9±1.8	88.5±2.6	—	2.6±2.3	69.2±1.4	78.6±1.1	—	1065±105	8
Ontario									
JP	7.5±2.0	0.0	83.2±1.9	9.3±1.6	—	—	62.9±1.9	2445±128	4
JPbs	29.2±3.9	3.6±2.3	64.1±4.9	3.0±1.5	51.9±0.8	—	65.2±0.9	2450±240	3
MW	6.7±1.4	30.7±7.0	48.2±6.4	14.4±6.1	—	66.2±2.8	62.3±1.9	1300±168	4
MWbs	26.0±4.8	27.1±3.6	44.0±10.9	2.9±2.5	50.6±3.8	64.6±1.4	68.4±2.0	2463±238	2
TA	0.0	95.2±1.2	0.7±0.7	4.1±0.9	—	68.7±1.0	—	780±43	5
TAbs	20.6±3.7	68.8±4.3	3.5±1.9	7.0±1.9	55.8±1.2	65.5±0.9	—	2045±205	4

*Values are means ± SEs.

†Abbreviations are as follows: BS, black spruce; MW, mixedwoods; TA, trembling aspen; JP, jack pine; JPbs, jack pine with a black spruce understory; MWbs, mixedwoods with a black spruce understory; TAbs, trembling aspen with a black spruce understory.

‡Other species consist of jack pine and balsam fir in Quebec, and of balsam fir, white spruce, and white birch in Ontario.

§Total density includes class 1 snags (see text for details).

pen and from 51 to 58 years old for black spruce (Table 1). A completely randomized sampling design was deployed.

Sampling and measurements

For both study areas, all sample plots were circular with an area of 400 m^2 with at least a 5 m buffer zone of the same composition. In each plot, all trees >5 cm diameter at breast height (DBH, 1.3 m) were numbered and measured for species, DBH, and height. Heights were measured using a Vertex clinometer. To assess plot density, all snags were also numbered and their decay classes noted to identify snags belonging to decay class 1 (i.e., recent snags mostly intact in branches, bark, and top). Mean breast height age was determined by coring a subsample of 20–40 trees in each plot. The cores were then measured and analyzed using a Velmex sliding-stage micrometer and TSAPWin (F. Rinn Engineering Office, Heidelberg, Germany) software along with COFECHA (Grissino-Mayer 2001). Measurements and sampling took place in June 2006 for the Quebec study and in May 2007 for the Ontario study.

Similarity of sites

To ensure that all sites were of similar quality in each region, we selected stands carefully according to the following criteria. All selected stands were upland sites with no or very little slope. All stands in the same study area had the same moisture regime (mesic in Ontario and subhygric in Quebec) and were on the same kind of deposits (clay in Quebec and tills in Ontario, see Study areas).

Similarity of sites was then validated by soil intrinsic physical and chemical properties (i.e., soil textures, cation exchanged capacity, and total nitrogen and carbon contents of the mineral layer at a depth of 35–55 cm; J. Laganière, Natural Resources Canada, Sainte Foy, Quebec, unpublished data). No significant differences could be detected among composition types at an error threshold of 0.1 using analyses of variance, except for clay percentage in the Ontario study. However, none of our response variables (individual tree carbon content, total stand carbon content, and height/diameter (H/D) ratios) appeared to be affected by any of the soil variables. Thus, soil variables had no influence on our analyses, which confirmed that all sampled stands within a study area were comparable.

Data analysis

Carbon calculation

The aboveground biomass of each tree was estimated from DBH and height with the allometric equations established by Lambert et al. (2005). Carbon was assessed from biomass with the mean carbon content values provided by Lamlom and Savidge (2003): spruce, 0.5039 kg C·kg^{-1}; jack pine, 0.504 kg C·kg^{-1}; trembling aspen, 0.4709 kg C·kg^{-1}; white birch, 0.4837 kg C·kg^{-1}; and balsam fir, 0.5008 kg C·kg^{-1}. Given that no such values were available for black spruce, we used that of white spruce in our calculations.

Statistical analyses for the Quebec study

For each species, differences in carbon content and H/D ratio (potential indicator of competition for light) at the individual tree level were tested among composition types with total stand density as covariants in hierarchical mixed-effect linear models (Pinheiro and Bates 2000) with composition nested in block as the random effect. Because class 1 snags can be considered as having been influential on stand growth until recently, they were included in total plot density. Interaction between composition and density was removed when it was insignificant at a threshold of 0.1. Differences in total stand carbon content were tested similarly by summing all individuals within the stand. Tree density without snags was used as a covariate. Comparisons between the individual levels of each factor were processed using Wald's t tests. Given that we had to discard some improper sites from the analyses, we were unable to retain a balanced design, thus decreasing the statistical power of our tests. To counterbalance this, we chose to use a 0.1 error threshold for all of our analyses to decrease the risk of making type II errors. Otherwise, this risk could have been too high particularly in the Ontario study, where the number of replicates was lower because of a higher number of composition types.

To test for a positive, negative, or neutral effect of MW on carbon pools at the stand level, observed carbon values in MW plots were compared for each block with expected carbon values. The calculation of the expected carbon values (C_{Exp}) is based on the following: if there is no composition effect on the total stand carbon content, then the carbon content in MW plots should follow the "additive line" displayed in Fig. 1. This corresponds to the C_{Exp} value that appears on the line and is the null hypothesis. If the observed carbon value in MW for the same proportion of species is significantly higher or lower than C_{Exp}, then we have a positive or negative mixture effect, respectively.

The following equation is used to calculate C_{Exp}:

$$[1] \qquad C_{\mathrm{Exp}} = (\alpha \times p\mathrm{Bs}_{\mathrm{MW}}) + (\beta \times p\mathrm{Ta}_{\mathrm{MW}})$$

where $p\mathrm{Bs}_{\mathrm{MW}}$ is the proportion of spruce density in MW (i.e., Bs refers to the individual trees and BS refers to the plots), $p\mathrm{Ta}_{\mathrm{MW}}$ is the proportion of aspen density in MW, and α and β having the same meaning as in Fig. 1.

Because the BS and TA plots were not 100% black spruce and 100% trembling aspen, respectively, we do not know the α and β values, but they can be derived from the BS and TA plots:

$$[2] \qquad C_{\mathrm{BS}} = (\alpha \times p\mathrm{Bs}_{\mathrm{BS}}) + (\beta \times p\mathrm{Ta}_{\mathrm{BS}})$$

$$[3] \qquad C_{\mathrm{TA}} = (\alpha \times p\mathrm{Bs}_{\mathrm{TA}}) + (\beta \times p\mathrm{Ta}_{\mathrm{TA}})$$

where C_{BS} is the carbon content in the BS plot, C_{TA} is the carbon content in the TA plot, $p\mathrm{Bs}_{\mathrm{BS}}$ is the proportion of spruce density in the BS plot, $p\mathrm{Ta}_{\mathrm{BS}}$ is the proportion of aspen density in the BS plot, $p\mathrm{Bs}_{\mathrm{TA}}$ is the proportion of spruce density in the TA plot, and $p\mathrm{Ta}_{\mathrm{TA}}$ is the proportion of aspen density in the TA plot.

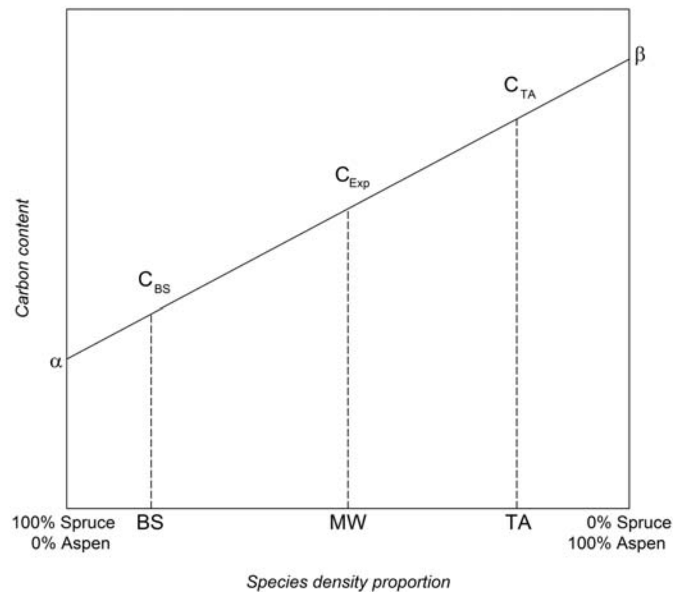
The solutions derived from eqs. 2 and 3 for α and β are

$$[4] \qquad \alpha = \frac{\left((C_{\mathrm{BS}} \times p\mathrm{Ta}_{\mathrm{TA}}) - (C_{\mathrm{TA}} \times p\mathrm{Ta}_{\mathrm{BS}}\right)}{\left(p\mathrm{Ta}_{\mathrm{TA}} \times p\mathrm{Bs}_{\mathrm{BS}}) - (p\mathrm{Bs}_{\mathrm{TA}} \times p\mathrm{Ta}_{\mathrm{BS}}\right)}$$

$$[5] \qquad \beta = \frac{C_{\mathrm{TA}} - (\alpha \times p\mathrm{Bs}_{\mathrm{TA}})}{p\mathrm{Ta}_{\mathrm{TA}}}$$

We computed α and β and then C_{Exp} for each block individually. The expected and observed carbon values were then compared using a paired Student's t test with an error threshold of 0.1. The same principle was applied to compare black spruce and trembling aspen carbon contents instead of total carbon contents. However, in these cases, the additive line was defined by the single-species plot of the considered species (BS plot for spruce and TA plot for aspen) and by a theoretical plot with 0% of the considered species and, thus, with no carbon of this species, which corresponded to the origin of the graph.

Fig. 1. Graphical representation of the null hypothesis for stand-level carbon comparisons: carbon content in black spruce (BS), mixedwood (MW), or trembling aspen (TA) plots along species density proportion. C_{BS} and C_{TA}, carbon contents in BS and TA plots, respectively; α and β, carbon contents in pure black spruce and pure trembling aspen plots, respectively. See text for details.



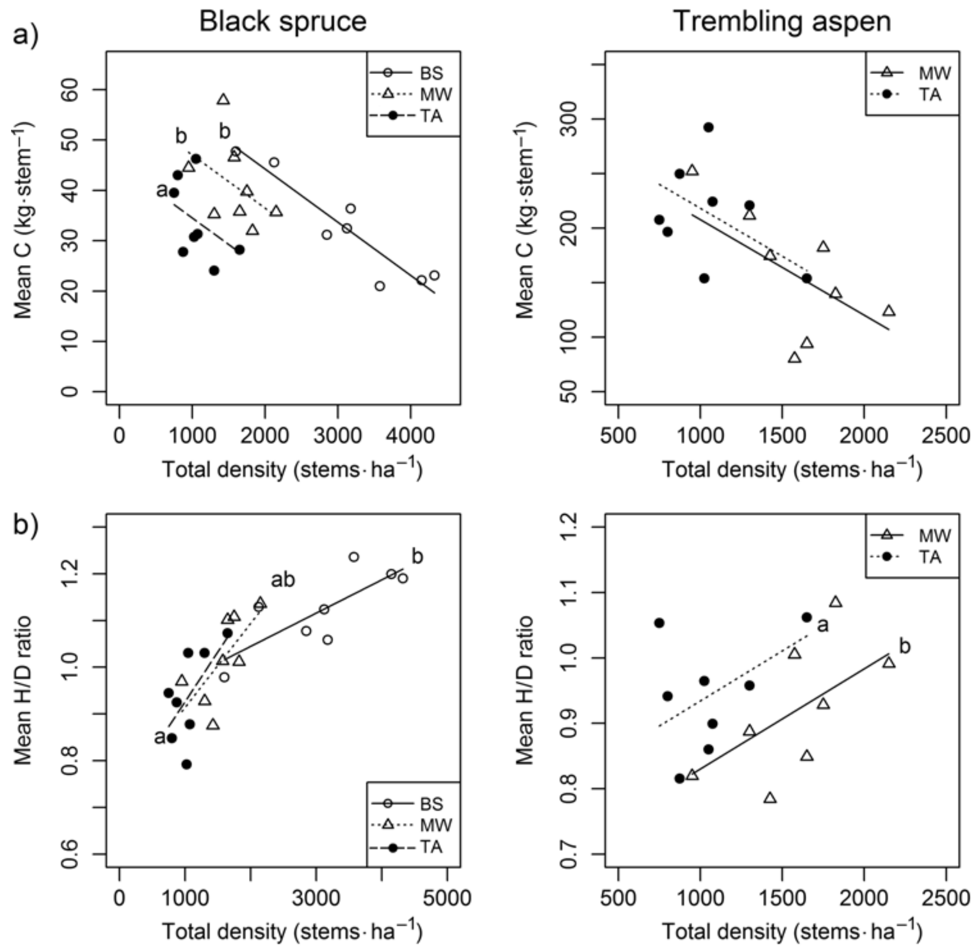
The species other than aspen and spruce were not included in this analysis. We excluded them from the carbon content and the species density proportion.

Statistical analyses for the Ontario study

These analyses were similar to those conducted for the Quebec data, except that three species were studied instead of two and that no random block effect could be included in the mixed linear models. Thus, the random effect in this case was only the individual plots to take into account the nonindependence of trees within the same plot. Comparisons of expected versus observed values in MW were also conducted similarly than in the Quebec study but by separately analyzing plots without black spruce subcanopy (TA and JP means vs. MW) from one side and plots with black spruce (TAbs and JPbs means vs. MWbs) from the other side; thus, we studied only pine and aspen responses, and reduced black spruce to a binary factor (absence–presence). This was necessary because no black spruce dominated stands could be sampled in the Ontario study. TAbs versus TA and JPbs versus JP were also compared but by using only aspen and pine carbon values and assuming a null amount of carbon of these species in the nonsampled theoretical pure black spruce plot used for expected value calculations. Because there was no block here, a single value of α and β was computed from all the single-species plots for each analysis and then used separately for each MW (or MWbs) plot to compute C_{Exp} values depending on the proportion of each species in the mixed plot. Thus, we could generate pairs of observed and expected values to compare in the t test.

All statistical analyses were performed using R software version 2.6.1 (R Development Core Team 2007).

Fig. 2. (*a*) Mean tree carbon contents and (*b*) mean tree height/diameter (*H*/*D*) ratios of black spruce and trembling aspen in relation to density and composition in the Quebec study. Lines with different letters are significantly different for the composition type effect or the composition × density interaction effect at α = 0.1.



Results

Quebec study

Individual tree level

Mean individual carbon content of both species decreased with increasing stand density (Fig. 2*a*, Table 2). Individual carbon content of black spruce was higher in BS and MW stands than that in TA stands (Fig. 2*a*, Table 2). Because only a few aspen stems were found in BS plots, trembling aspen individual responses were compared only between MW and TA plots and showed no difference in mean carbon content between the two stand types (Fig. 2*a*, Table 2).

Mean *H*/*D* ratios of both species increased with stand density (Fig. 2*b*, Table 2). For black spruce, this increase was lower in BS stands than TA stands with MW stands being intermediate (Fig. 2*b*, Table 2). For trembling aspen, *H*/*D* ratios were lower in MW than in TA stands (Fig. 2*b*, Table 2).

Table 2 gives the global effects for each variable rather than the individual comparisons.

Stand level

Density had no effect on total carbon content at the stand level, but carbon content differed among three stand types. It was higher in TA, lower in BS, and intermediate in MW (Fig. 3, Table 2).

Comparisons of expected versus observed values in MW plots showed a smaller amount of spruce carbon in MW than expected, whereas aspen and total stand carbon contents did not differ between expected and observed values (Fig. 4).

Ontario study

Individual tree level

Results for each species were compared only for the compositions where they were expected to be found abundantly (i.e., only JPbs, MWbs, and TAbs stands for black spruce; TA, TAbs, MW, and MWbs for trembling aspen; and JP, JPbs, MW, and MWbs for jack pine). Black spruce mean carbon content was smaller in MWbs than in TAbs stands (Fig. 5*a*, Table 2). Mean carbon content per tree for trembling aspen and jack pine decreased with increasing density. This decrease was stronger for jack pine in MW than in JPbs and MWbs stands. There was no response to composition for trembling aspen (Fig. 5*a*, Table 2).

Black spruce mean *H*/*D* ratios increased with increasing density (Fig. 5*b*, Table 2). These ratios were also smaller in MWbs plots than in JPbs plots (Fig. 5*b*, Table 2). Those of

Table 2. Results of analyses of covariance for the mixed linear models.

Dependent variable and fixed effect*	*F*	*P*
Quebec		
Black spruce mean C		
Density	31.239	<0.001
Composition	7.040	0.01
Black spruce mean *H*/*D*		
Density	36.216	<0.001
Composition	0.358	0.708
Composition × density	2.826	0.107
Trembling aspen mean C		
Density	4.767	0.072
Composition	1.568	0.257
Trembling aspen mean *H*/*D*		
Density	5.607	0.056
Composition	4.213	0.086
Total C		
Density	0.007	0.935
Composition	4.808	0.029
Ontario		
Jack pine mean C		
Density	34.531	0.002
Composition	1.080	0.437
Composition × density	4.104	0.081
Jack pine mean *H*/*D*		
Density	3.272	0.108
Composition	0.587	0.641
Black spruce mean C		
Density	0.861	0.396
Composition	3.616	0.107
Black spruce mean *H*/*D*		
Density	5.989	0.058
Composition	2.556	0.172
Trembling aspen mean C		
Density	3.840	0.079
Composition	1.258	0.341
Trembling aspen mean *H*/*D*		
Density	0.470	0.509
Composition	0.213	0.885
Total C		
Density	0.459	0.509
Composition	1.126	0.388

*C, carbon content; *H*/*D*, height/diameter ratio.

jack pine and trembling aspen responded neither to density nor composition (Fig. 5*b*, Table 2).

Stand level

Total carbon content did not change with density but was lower in MWbs than in TA stands (Fig. 6, Table 2). The paired *t* tests between expected and observed carbon values showed a negative effect for trembling aspen in MW plots and a positive effect for jack pine in JPbs plots (Fig. 7).

Discussion

Carbon pools in the overstory were highly dependent on forest composition. Trembling aspen dominated stands are the most efficient ones for net carbon accumulation 90 years

Fig. 3. Carbon partition among black spruce, trembling aspen, and other species for each composition at the stand level in the Quebec study. See Table 1 for the other species. Bars with different letters are significantly different among the three composition types for total stand carbon at $\alpha = 0.1$. Error bars are SEs and are calculated from total carbon.

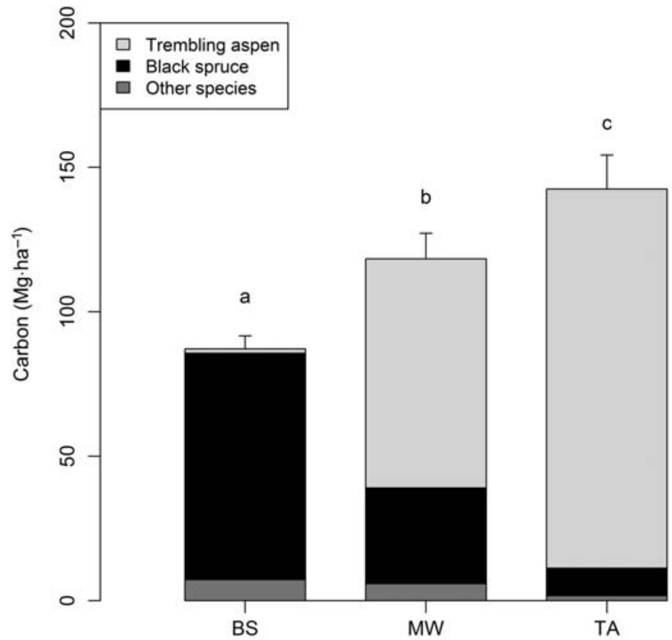


Fig. 4. Expected and observed carbon values for black spruce and trembling aspen in MW stands of the Quebec study. Bar sections with different letters are significantly different among the species at $\alpha = 0.1$. Error bars are SEs and are calculated from total carbon.

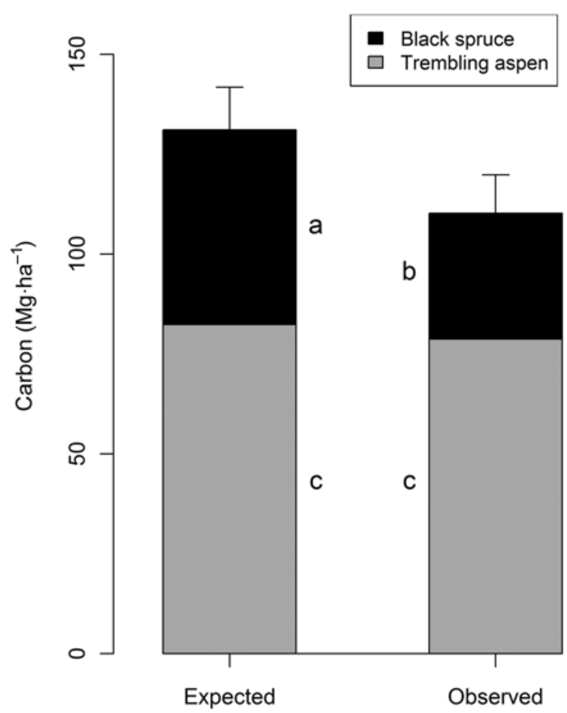


Fig. 5. (*a*) Mean tree carbon contents and (*b*) mean tree *H*/*D* ratios of black spruce, jack pine and trembling aspen in relation to density and composition, in the Ontario study. See Table 1 for stand abbreviations. Lines with different letters are significantly different among composition types or for the composition × density interaction effect at α = 0.1.

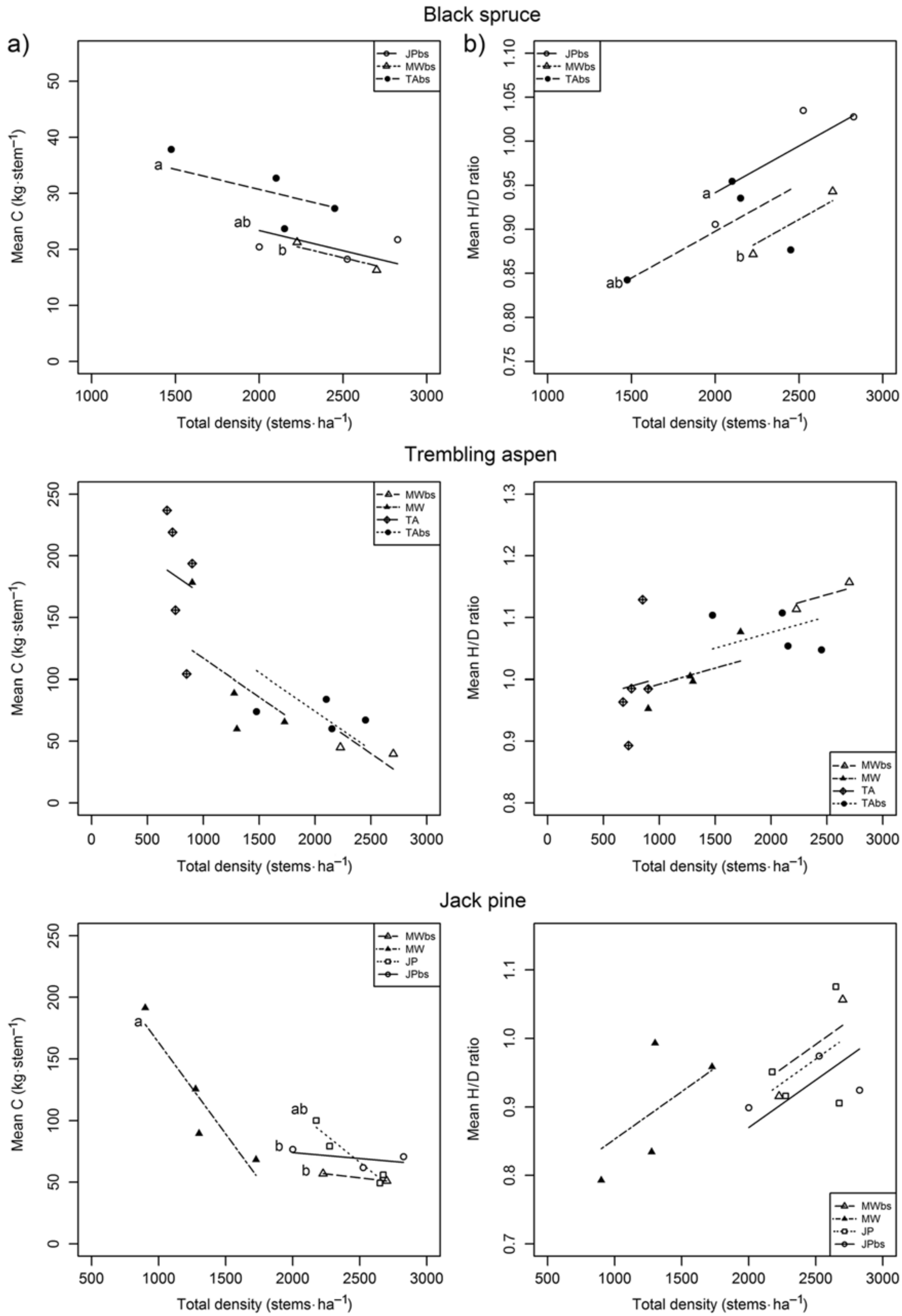
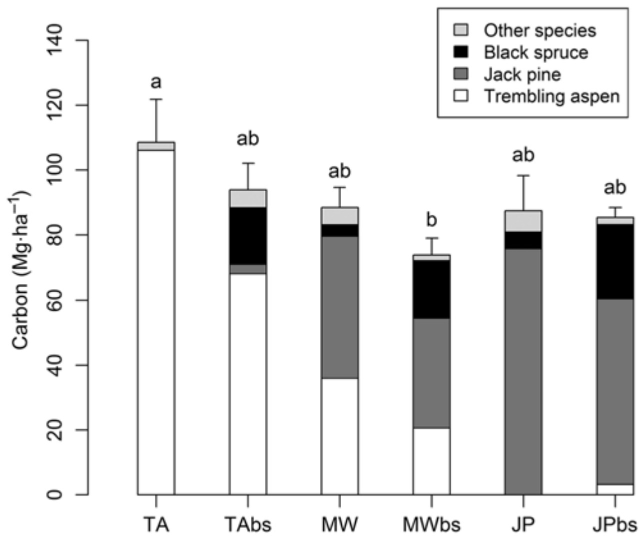


Fig. 6. Total stand carbon partitioned by species in relation to stand composition type for the Ontario study. Bars with different letters are significantly different at $\alpha = 0.1$ Error bars are SEs and are calculated from total carbon.



following fire in the Quebec study (142 Mg C·ha^{-1}), whereas black spruce stands are less efficient (87 Mg C·ha^{-1}). Given the lower commercial value of trembling aspen, spruce–aspen mixedwood could be considered as a good compromise (118 Mg C·ha^{-1}). Perhaps because of the absence of pure black spruce stands, differences in the Ontario study are less pronounced, ranging from 74 Mg C·ha^{-1} (MWbs) to 108 Mg C·ha^{-1} (TA).

Black spruce and trembling aspen relationships

The accumulation of a thick organic layer in black spruce stands (the paludification process) is slower when aspen is present (Fenton et al. 2005), and the surface soil concentrations of exchangeable cations (K, Ca, and Mg) have been shown to increase with aspen presence in black spruce stands (Légaré et al. 2005*b*). Thus, the presence of aspen may favour the development of a warmer and nutrient-rich soil that should potentially increase spruce growth (Thiffault and Jobidon 2006). Such a facilitation effect is not observed in our Quebec experiment, because black spruce individual carbon pools in mixedwood plots are not different from those in black spruce plots for equivalent densities and are even lower in trembling aspen plots. Using forest inventory data, Légaré et al. (2004) found a positive effect of aspen on black spruce individual growth only when aspen represents <40% of stand basal area. Because our MW plots are above this threshold (Table 1), the absence of an effect in MW is consistent with the results of Légaré et al. (2004). The following trade-off hypothesis could explain our results: the positive impact of aspen on black spruce due to improved soil conditions is gradually offset as aspen proportion increases. This increasing negative impact could be linked to competition for light, because trembling aspen always overtops black spruce. The fact that the density effect on black spruce *H*/*D* ratios is stronger in TA stands could confirm this hypothesis. However, this result must be interpreted carefully because tree morphology is not only driven by competition for light, but also by wind exposure (Holbrook and Putz 1989; Meng et al. 2008). Because overtopping from aspen generates both increased shade and shelter from the wind, these two factors potentially explaining the response of *H*/*D* ratios to density and composition are, unfortunately, indistinguishable in the Quebec study. Increased competition for soil resources could also be an explanation of aspen negative impact on spruce in TA stands.

On the Ontario side, spruce *H*/*D* ratios are smaller under a mixed jack pine – trembling aspen canopy than under jack pine (another shade-intolerant, overtopping species). Because wind sheltering provided to black spruce is not likely to change between pine or aspen, this suggests that spruce might actually benefit from the leafless periods of aspen, as was hypothesized by some authors (Green 2004). However, in this case, spruce *H*/*D* ratios should also be significantly smaller in TAbs plots, which is not the case. This result might then be only an artefact due to the small number of proper MWbs replicates left for analysis (only two instead of four for most of the other composition types). Thus, it is difficult to tell whether the gain in black spruce individual growth in TAbs plots can be partly attributed to this reduction of shade during the aspen leafless period and, thus, to niche separation, or only to the positive effect of aspen on soil conditions compared with jack pine (Longpré et al. 1994).

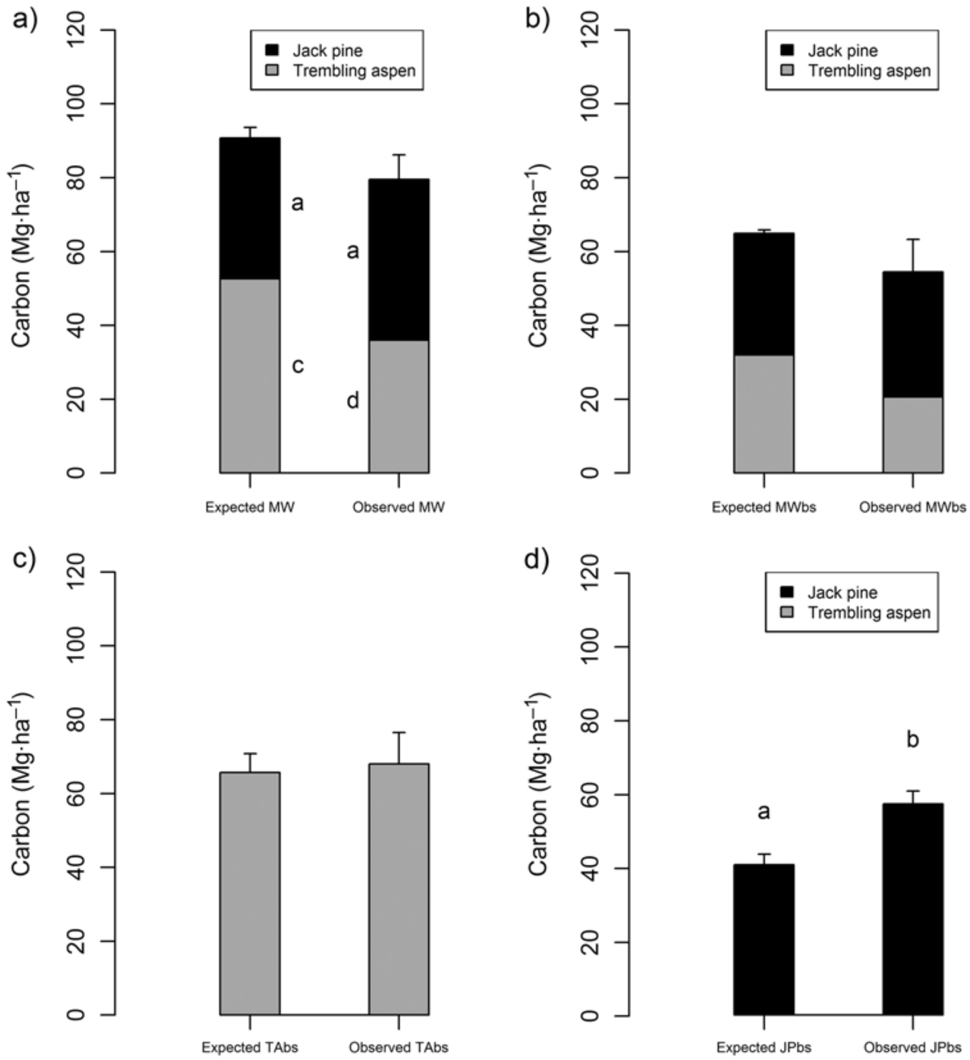
Carbon pools in trembling aspen individual trees do not respond to composition in either the Quebec or the Ontario study. Aspen *H*/*D* ratios in the Quebec study are smaller in MW plots compared with TA plots. This would only confirm the obvious niche separation: aspen trees suffer less from light competition when neighbouring a spruce tree than an aspen tree. However, this reduced competition is not followed by any increase in carbon content. Considering that trembling aspen is an early successional species with high resource requirements, another trade-off hypothesis seems likely in this case: the benefit of growing with a less competitive species is offset by the negative impact of black spruce on soil conditions (Légaré et al. 2005*b*).

Based on the absence of individual responses in mixedwoods from both species, we would expect a purely neutral effect at the stand level (i.e., MW values would be linearly predictable from those of TA and BS plots). This is generally the case except for black spruce, for which values in MW plots are significantly lower than expected from TA and BS plots. Nevertheless, this can be explained by the strongly reduced density of black spruce in the presence of aspen: one aspen stem occupies a space in a MW stand that would be occupied by several spruce stems in a BS plot. This loss of "growing space" for black spruce in MW accounts for the loss of spruce carbon compared with what was expected. However, this loss is apparently too weak to be significant when total stand carbon contents (i.e., for all species) are compared.

Trembling aspen and jack pine relationships

Results from the Ontario study showed no effect of jack pine presence on trembling aspen, whereas the interaction results for jack pine individual carbon contents showed that the density effect on jack pine was stronger in MW plots than in JPbs (and MWbs, but see the remark made previously on these) plots. Because pine is in competition with

Fig. 7. Expected and observed total stand carbon of (*a*) jack pine and trembling aspen in MW stands, (*b*) jack pine and trembling aspen in MWbs stands, (*c* and *d*) the dominant overstory species in (*c*) TAbs (i.e., trembling aspen) and (*d*) JPbs (i.e., jack pine) stands. Bars or bar sections with different letters are significantly different among species at $\alpha = 0.1$. Error bars are SEs and are calculated from total carbon.



fast-growing aspen in MW and with black spruce in JPbs, this result is not surprising. Although jack pine *H*/*D* ratios did not react to composition, these results might suggest that aspen could be a slightly better competitor against pine than pine is against itself. However, this difference was too weak to have an impact at the stand level, because expected and observed values in MW and MWbs are not significantly different for jack pine, which confirms previous results demonstrating the absence of jack pine response to trembling aspen presence (Longpré et al. 1994). This is easily explained by the fact that these two species share the same niche: fast-growing, shade-intolerant species with similar growth and space occupancy patterns (Béland et al. 2003), whereas the broadleaf effect on soil conditions did not affect jack pine growth compared with competition for light (Longpré et al. 1994; Béland and Bergeron 1996). Interestingly, there was a negative effect on trembling aspen in MW at the stand level that was not statistically detected at the tree level, but which confirmed the tendency that could be observed (see Fig. 5). Even though jack pine effect on soil properties is not comparable with that of black spruce (Crawford et al. 2003), it could have made a difference on the low-fertility sandy soils of the Ontario study (Ste-Marie et al. 2007).

Finally, the positive effect on jack pine at the stand level in JPbs plots is probably due to the fact that because of the differences in spatial occupancy between pine and spruce, 50% of a stand's density does not represent the same number of stems whether JP or JPbs plots are considered. Thus, this result only represents a gain in space for jack pine in JPbs plots, which is similar to the loss of space for black spruce in MW plots in the Quebec study.

Conclusion

Our study showed that interspecific interactions vary depending on the considered species. Thus, the mixture effect seems detrimental when two competitive species are mixed (trembling aspen with jack pine). The adverse effect of black spruce on soil condition likely explains why a more beneficial result has not been observed here when complementary species were mixed (trembling aspen with black spruce). Thus, it may be possible that mixing shade-intolerant species with slow-growing, shade-tolerant ones that would not have such a detrimental effect on forest floor properties (e.g., white spruce or balsam fir) could lead to significantly higher carbon pools in mixedwoods for the shade-intolerant species. It must also be remembered that although they contain less spruce carbon, spruce–aspen mixedwoods have a greater amount of total carbon compared with pure black spruce stands and, thus, could be a potentially interesting compromise between carbon sequestration and spruce yield.

Previous results from Légaré et al. (2004) also point out the importance of the proportion of the mixture, because black spruce volume was greater at the individual and stand levels when aspen represented between 5% and 40% of stand basal area. This strongly suggests that some specific proportion of tree mixtures may have a positive impact on aboveground carbon sequestration. In the present case, the potentially beneficial soil effect of trembling aspen in 90-year-old black spruce stands did not seem sufficient to have an impact on black spruce growth; however, in the long term, it might prevent or delay the stands from becoming unproductive as a result of paludification, as documented by Simard et al. (2007) on adjacent sites. On the other hand, the jack pine – black spruce mixture does not seem to have much potential, because the overtopping of spruce by pine may not be counterbalanced by any improvement in soil conditions. However, the positive long-term effect on carbon sequestration in spruce–aspen mixtures could be counterbalanced by the lower carbon accumulation in the soil organic layer as compared with old paludified black spruce stands. This is why a definitive answer concerning the potential of boreal mixedwoods as carbon sinks will need to consider all pools and fluxes. The information provided by these ongoing studies may also shed light on some of the issues raised in this paper by confirming or refuting the hypotheses proposed to explain our results.

Acknowledgements

We thank Eric Boucher and Timo Puiras for field assistance, Brian Brassard and Stephen Hart for help with finding the Ontario sites, Pamela Cheers for revising this manuscript, and anonymous reviewers for their helpful comments. We are also grateful to Tembec Inc. for allowing us access to the Quebec sites and Abitibi Bowater for the Ontario ones. This study was supported by the Natural Sciences and Engineering Research Council – Université du Québec en Abitibi-Témiscamingue – Université du Québec à Montréal Industrial Chair in Sustainable Forest Management and a strategic grant from the Natural Sciences and Engineering Research Council of Canada.

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