The influence of boreal tree species mixtures on ecosystem carbon storage and fluxes

Jérôme Laganière [a,*], Xavier Cavard [b], Brian W. Brassard [c], David Paré [a], Yves Bergeron [d], Han Y.H. Chen [c]

[a] Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, Québec, QC G1V 4C7, Canada
[b] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden
[c] Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada
[d] Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, QC J9X 4E5, Canada

ARTICLE INFO

ABSTRACT

Plant species mixtures are often seen as being able to achieve higher productivity and carbon (C) sequestration than their single-species counterparts, but it is unclear whether this is true in natural forests. Here, we investigated whether naturally-regenerated mixtures of common North American boreal tree species were more productive and stored more C than single-species stands. We also examined how closely the different C pools and fluxes were interrelated and whether these relationships varied with species composition. Single- and mixed-species stands of trembling aspen, black spruce and jack pine on mesic sites were selected in two regions of the Canadian boreal forest to assess aboveground and belowground productivity and C storage. Although previous studies conducted in these stands found synergistic effects of tree species mixtures on specific C pools and fluxes, such as higher organic layer C stocks and higher fine root productivity in some mixtures, no effects were detected on combined C pools or fluxes at the ecosystem level in the current study. Aspen abundance was linked with higher aboveground tree productivity, higher aboveground living biomass and higher soil heterotrophic respiration, indicating that aspen acts as a key driver of ecosystem C storage and fluxes in these natural forest ecosystems, more so than species richness. However, our results do not rule out the possibility of increased productivity and C storage in mixed stands under environmental conditions or stand developmental stages that are different from the ones studied here. Furthermore, when the entire forest ecosystem is considered (not only tree parts), synergistic effects of tree species mixtures may be more difficult to observe because the beneficial effect of species mixing on one specific C pool may be counterbalanced by a negative effect on another pool.

Crown Copyright © 2015 Published by Elsevier B.V. All rights reserved.

1. Introduction

Species mixtures are common in natural forests, and it has been hypothesized that mixed-species stands could be more productive than single-species stands because resources are used more completely by the companion species (Hooper et al., 2005; Kelty, 2006). Complementarity can come from niche partitioning and/or facilitation among species with different functional traits, thereby decreasing competition in diverse communities (Tilman, 1999; Brooker et al., 2008). Most studies investigating species mixture-productivity relationships using trees were conducted in plantations. Empirical evidence of wood volume production gain in naturally-regenerated mixedwoods is sparse and controversial.

For example, aspen–conifer mixtures were reported as more productive than single-species stands in studies by MacPherson et al. (2001) and Légaré et al. (2004), but less productive in the Edgar and Burk (2001) study. Using large datasets of forest inventory plots in natural systems, Paquette and Messier (2011) and, more recently, Vilà et al. (2013) showed that mixed-species stands had higher tree productivity and higher wood volume, respectively, than single-species stands, though neither of these studies controlled for the potentially better edaphic conditions on which mixed stands are often established. A global meta-analysis of tree species diversity effects on aboveground productivity indicates an average 24% productivity gain in mixed-species stands compared with monocultures, and the positive diversity effects are dependent on the number of species in the mixtures, species evenness, life-history trait variation, and the stage of stand development (Zhang et al., 2012).

Most studies assessing tree mixture-productivity relationships have focused on merchantable wood biomass or stemwood C, probably due to its economic importance. However, C is stored in a variety of pools beyond stem wood, including tree roots, understory vegetation, coarse woody debris and soil. Fine roots as well as understory plants may each represent over one third of the total ecosystem production in some forests (Jackson et al., 1997; Bisbee et al., 2001; Connell et al., 2003). Soil is also a C pool of major importance given that more C is stored in the soil than in plant biomass (Lal, 2005), though only the upper soil profile is usually affected by current vegetation (Laganière et al., 2013; Vesterdal et al., 2013). To our knowledge, there are no reported studies that have examined tree species mixture effect on C storage and sequestration at the entire ecosystem level (i.e. not only aboveground tree parts) in natural systems.

In this synthesis study, we used empirical data from single-and mixed-species stands of two regions of the Canadian boreal biome, some of which have already been published (Cavard et al., 2010; Brassard et al., 2011b; Cavard et al., 2011a; Cavard et al., 2011b; Laganière et al., 2012; Brassard et al., 2013; Laganière et al., 2013), to investigate the links between ecosystem C pools (organic layer, mineral soil, dead and live coarse, medium and fine roots, aboveground live tree parts, snags and understory vegetation) and fluxes (aboveground tree productivity, fine root productivity, understory productivity and soil heterotrophic respiration) and tree species mixture effects. Specifically, we wished to address the following questions: (1) Do mixed-species stands have greater ecosystem C storage and sequestration than single-species stands? (2) How are the sizes of the different C pools related to tree species composition? (3) Is higher ecosystem C storage associated with higher ecosystem production and/or slower decomposition?

2. Material and methods

2.1. 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 mean annual precipitation (MAP) of 712 mm and a mean annual temperature (MAT) of 2.5 °C (Environment Canada, 2014). Four stands dominated by jack pine, *Pinus banksiana* Lamb. (abbreviated as "JP"), five stands dominated by trembling aspen, *Populus tremuloides* Michx. (abbreviated as "TA"), and thirteen mixed-species stands of jack pine, aspen and/or black spruce, *Picea mariana* (Mill.) BSP (abbreviated as "BS"), (see

Table 1) were selected for sampling in a 250 km² area with a maximum distance of 30 km between stands (total: 22 stands). The understory vegetation in the jack pine stands consisted mainly of the herbs *Cornus canadensis* L., *Maianthemum canadensis* Desf. and *Linnea borealis* L. and feathermosses, 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 (Bartels and Chen, 2013). 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 1923 wildfire (Senici et al., 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 MAP of 890 mm and MAT of 0.7 °C (Environment Canada, 2014). Six stands dominated by black spruce, eight stands dominated by trembling aspen, and seven mixed stands comprising a relatively uniform component of both tree species were selected for sampling in a 100 km² area with a maximum distance of 10 km between stands (total: 21 stands). The understory vegetation in the black spruce stands consisted mainly of the herbs *C. canadensis*, *Rhododendron groenlandicum* (Oeder) Kron and Judd and *Vaccinium* spp. and big red stem moss (*Pleurozium schreberi* (Bird.) Mitt.). 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*, while 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 1916 wildfire (Bergeron et al., 2004).

2.2. Sampling design

Similar to other studies that investigated tree species mixture effects in naturally established mature stands (e.g. Wang et al., 2002; Brassard et al., 2008), the criteria for stand selection were that mixed-species stands should have relatively equal proportions of component tree species by stand basal area, while for single-species stands, the basal area of a single tree species would be >80% of total stand basal area (Table 1).

Table 1

Overstory characteristics and mean annual soil temperature (at 5 cm depth) of the study plots (mean ± 1 SE). Other species consist of balsam fir, white spruce and paper birch in the Ontario region and jack pine and balsam fir in the Quebec region.

Stand type	Number of stands	Total basal area (m² ha⁻¹)		Total density (stems ha⁻¹)		Species composition by basal area (%)								Soil temperature (°C)	
						BS		TA		JP		Other species			
Ontario															
JP	4	49.4	(3.6)	2445	(128)	7.5	(2.0)	0.0	(0.0)	83.2	(1.9)	9.3	(1.6)	4.8	(0.2)
TA	5	43.3	(3.8)	780	(43)	0.0	(0.0)	95.2	(1.2)	0.7	(0.7)	4.1	(0.9)	5.5	(0.1)
JP + BS	3	47.6	(1.2)	2450	(240)	29.2	(3.9)	3.6	(2.3)	64.1	(4.9)	3.0	(1.5)	4.5	(0.1)
TA + BS	4	53.9	(3.3)	2045	(205)	20.6	(3.7)	68.8	(4.3)	3.5	(1.9)	7.0	(1.9)	4.8	(0.1)
JP + TA	4	44.6	(2.0)	1300	(168)	6.7	(1.4)	30.7	(7.0)	48.2	(6.4)	14.4	(6.1)	5.4	(0.1)
JP + TA + BS	2	44.3	(1.9)	2463	(238)	26.0	(4.8)	27.1	(3.6)	44.0	(10.9)	2.9	(2.5)	4.4	(0.1)
Quebec															
BS	6	43.4	(2.3)	3115	(380)	89.4	(4.2)	1.8	(0.7)			8.8	(4.0)	4.7	(0.1)
TA	8	57.7	(3.6)	1065	(105)	8.9	(1.8)	88.5	(2.6)			2.6	(2.3)	4.9	(0.1)
BS + TA	7	52.2	(2.7)	1578	(128)	33.8	(3.6)	59.5	(3.5)			6.7	(1.6)	5.2	(0.1)

Note: BS, black spruce; JP, jack pine; TA, trembling aspen. Numbers in parentheses are ±1 SE. Modified from Cavard et al. (2011).

To ensure that stand type differences in dependent variables are the result of differences in tree species composition and their associated understory, we selected stands in each respective region with similar site conditions: climate, soil type and texture, parent material, drainage, topography and time since fire. Similarity of drainage class, parent material and soil type were 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 >1 ha in area, fully stocked and visually homogeneous in structure and composition. Thus, any variation in dependent variables between stand types is assumed to result from differences in tree species composition and in their associated understory. In each selected stand, a 400 m^2 circular plot was established and the aboveground, belowground and soil components were sampled.

2.3. Aboveground data

2.3.1. Trees

Detail on the assessment of aboveground tree biomass and productivity can be found in Cavard et al. (2010) and in Cavard et al. (2011b), respectively. Briefly, in each plot, all live and dead trees with a diameter ⩾5 cm were identified at the species level and measured for DBH (diameter at breast height, 1.3 m) and height. Aboveground biomass of each tree (stem + bark + branches + foliage) was estimated using the allometric equations developed by Lambert et al. (2005). Aboveground tree productivity was estimated as the mean annual difference in biomass during the last 5 years of measurements based on a subset of 20–40 cored trees per plot. Biomass was expressed as C content using the mean C content values provided by Lamlom and Savidge (2003). Downed coarse woody debris were not assessed in the present study.

2.3.2. Understory vegetation

Understory plants refer to all non-tree plant species, plus tree seedlings and saplings with a DBH <5 cm. Grass, lichen and fungal biomass was negligible and, therefore, not considered in further analyses. Detail on the assessment of understory plant biomass and productivity can be found in Cavard et al. (2011a). Briefly, three 1 m^2 quadrats were established in each plot. Understory plants were measured in July and August 2007, and in July and August 2008. Main stem length or leaf length was measured, depending on the morphology of the plant species. We attempted to measure a feature of the plant species that would be strongly correlated to its biomass so that its biomass could be easily, as well as accurately, predicted from the measured morphological feature without destructive sampling. Aboveground parts were harvested in 2008, oven-dried for 48 h at 65 °C, and weighed. Bryophytes were also harvested at that time, with all species pooled together. Understory measurements were converted into biomass values and used to estimate total understory biomass in 2007. The difference between 2007 and 2008 understory biomass served as a proxy for understory production. For species that did not retain their aboveground parts during winter, production was considered equal to their biomass in 2008. Carbon was estimated at 50% of the dry biomass.

2.4. Belowground data

Fine root (⩽2 mm in diameter) and medium root (>2 to ⩽10 mm in diameter) biomass (live roots) and necromass (dead roots) were determined according to Brassard et al. (2011b). Within each plot, seven soil cores (6.75 cm in diameter) were randomly extracted from the forest floor surface to a mineral soil depth of 30 cm using a power auger in mid-July of 2007, which is generally regarded in northern forests as the period of maximum fine root biomass (Steele et al., 1997; Wang et al., 2003). Fine/medium root fragments were separated from the soil in the laboratory by sieving the soil

cores with water; they were then sorted by vitality class, i.e. live versus dead roots, according to Persson (1983) and Bennett et al. (2002). Live fine/medium roots were further divided into species classes using a combination of morphological characteristics (see Brassard et al. (2011b) for more details), but the total biomass is reported here. Total fine/medium root biomass and necromass was calculated at each site by summing the dry weight of live and dead fine/medium roots, respectively, in each soil core and scaling it up to per hectare. Annual fine root production was estimated based on the ingrowth core method (Steele et al., 1997; Hendricks et al., 2006). A power auger was used to drill holes at each site. A plastic mesh core was then inserted into each hole, filled with root-free soil (medium-textured sand) and covered with leaf litter. Ten ingrowth cores (7.75 cm in diameter, 30 cm in length) were installed at each site in October 2007 and removed after one calendar year. Roots were separated from the soil, dried and weighed, and no roots >2 mm in diameter were present in any of the ingrowth cores. Fine root production was not measured for any of the JP + TA + BS stands in ON, nor for BS stands in QC. To calculate the coarse root (>10 mm in diameter) biomass and necromass of individual trees and shrubs, we used allometric equations developed by Brassard et al. (2011a) and Bond-Lamberty et al. (2002) for trees/shrubs with DBH ⩾10 cm and <10 cm, respectively. Individual tree/shrub coarse root biomass and necromass estimates were then summed to the plot level and scaled up to per hectare (further details on the method used can be found in Taylor et al., 2014). The C content of coarse roots was assumed to be 50% of the dry biomass, whereas that of medium and fine roots was assumed to be 45% of the dry biomass (Seedre et al., 2014).

2.5. Soil data

2.5.1. Soil C stocks

Detail on the assessment of soil C stocks can be found in Laganière et al. (2013). Briefly, in June 2006, after complete soil thawing, four sampling points were randomly determined within each plot. At each sampling point, a 15 × 15 cm^2 section of the entire organic layer (i.e., 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 of the deep mineral layer (35–55 cm) was extracted. Soil bulk density was determined according to Maynard and Curran (2007). All field-moist soil samples were passed through 6- and 4-mm sieves for organic and mineral layer samples, respectively, and subsamples were analyzed for their C concentrations by dry combustion using a LECO CNS-2000 analyzer (Leco Corp., St. Joseph, MI, USA). C contents were then calculated by multiplying C concentrations with their respective soil bulk densities and sampling depths. For the purpose of this paper, all mineral soil C data were pooled by site to get an estimate of the whole soil profile (i.e. 0–55 cm).

2.5.2. Soil respiration

Detail on the assessment of soil heterotrophic respiration data can be found in Laganière et al. (2012). The small root exclusion method developed by Vogel and Valentine (2005) was used to determine soil heterotrophic respiration. Polyvinyl chloride collars (30 cm deep) were inserted into the soil to exclude small roots. Soil respiration was measured at three locations within each site during the growing season, once a month from June to September 2007, once a week in October 2007, and once in June 2008. CO_2 efflux from soil was measured by placing the soil chamber of a portable infrared gas analyzer (LI-6400, LI-COR Inc., Lincoln, NE, USA) above the collar. While CO_2 efflux was being measured, soil temperature

at a depth of 5 cm in the organic layer was recorded with a thermocouple. Temperature was also recorded every 4 h from June 2007 to June 2009 using temperature loggers inserted at a depth of 5 cm into the organic layer of each plot. These continuous temperature data were used to estimate soil respiration outside measurement periods using temperature–respiration relationships and to evaluate annual soil heterotrophic respiration. We used an Arrhenius-type model (Lloyd and Taylor, 1994) instead of the first-order exponential model used in Laganière et al. (2012) to fit the site-specific temperature–respiration relationships because the latter model tends to overestimate respiration for temperatures not covered by experimental data (Bond-Lamberty et al., 2004).

2.6. Data analysis

This synthesis study focused on non-additive synergistic effects brought about by tree species mixing and, more specifically, on transgressive overyielding, assuming climate change mitigation and increased ecosystem C storage are the primary goals of growing species in mixtures. Transgressive overyielding is observed when C stock/flux of mixed-species stands ($C_{1,2}$) is superior to that of both single-species stands ($C_{1,2} > C_1$ and $C_{1,2} > C_2$). To determine if total ecosystem C storage, individual C pools or fluxes varied among stand types within a region, we performed ANOVAs using SAS v9.3 (SAS Institute, Cary, NC, USA). However, non-transgressive overyielding or net mixture effect, which is the positive deviation of C storage observed in the mixture from the expected additive C values of single-species stands with corresponding species proportion p ($C_{1,2} > p_1C_1 + p_2C_2$), can also be estimated (see Pretzsch and Schütze (2009) for a thorough discussion on overyielding). Net mixture effect was calculated according to Cavard et al. (2010), except that tree basal area was used to estimate tree species proportion rather than tree density. The net mixture effect on total ecosystem C storage was calculated for the JP + TA mixture in ON as well as for the BS + TA mixture in QC. However the net mixture effect could not be calculated for the full range of stand composition studied because of data set limitations. It could not be calculated for other mixed-species stands in ON because no single-species black spruce stands were available (thus making it impossible to calculate a net mixture effect for mixed-species stands containing black spruce). Estimates of total C storage used in the calculation of the net mixture effect did not include medium and fine root C because these were determined for a subset of sites only (19 out of 42 sites). A paired t-test was performed to detect significant differences between observed and expected total C storage in mixtures. To meet the assumptions of normality and homoscedasticity, data were $\log_{10}$-transformed when necessary. The significance threshold was set at 0.05. To examine how closely the different C pools and fluxes were interrelated and whether these relationships varied with species composition, we performed two principal component analyses (PCA) on mean-centered data with aspen proportion of stand basal area as an explanatory variable, given the reported influence of aspen on ecosystem functions (Paré and Bergeron, 1995; Légaré et al., 2005; Laganière et al., 2009) and its wide distribution among stands of both regions studied. To capture more robust relationships, and because these relationships were similar across both regions, data from all stands were combined into a single PCA.

3. Results

3.1. C stocks

Total ecosystem C storage, i.e. the sum of all C pools investigated excluding medium/fine roots, did not differ significantly between stand types in both regions (Table 2). Higher C storage in mixed-species stands relative to both single-species stands (i.e. transgressive overyielding) was therefore not detected in any of the mixed-species stands. Furthermore, no net mixture effect (i.e. non-transgressive overyielding) was observed in the mixedwood stands for which single-species stands of the companion species were available (Fig. 1). Indeed, observed total ecosystem C values in mixed-species stands (JP + TA in ON and BS + TA in QC) were not significantly different from expected C values derived from a linear interpolation of C values found in single-species stands of companion species (t-tests: $P > 0.05$). However, when examined by individual C pools and C components (i.e. dead, living, aboveground, belowground), significant differences between stand types were found (Table 2). In the QC region, aboveground C was significantly higher in TA than in BS or BS + TA stands, while TA stands had the highest living C, followed by BS + TA and single-species BS stands. In the ON region, living C and aboveground C had the highest values in TA stands, but these were not significantly different relative to other stand types. Dead C and belowground C did not differ among stand types in either region.

Organic layer C stock was higher in all mixed-species stands than in single-species stands in the ON region, and higher in mixed-species BS + TA stands and single-species TA stands than in single-species BS stands in the QC region (Table 2; Fig. 2). Understory vegetation C stock was higher in single-species TA stands than in mixed-species JP + BS and JP + TA + BS stands in the ON region, while in the QC region, it was higher in single-species BS stands than in mixed-species BS + TA stands. In the QC region, coarse root C stock (dead and living) was higher in TA and BS + TA stands than in BS stands. Fine root C stock was also higher in mixed-species BS + TA stands than in single-species TA stands. Single-species TA stands had the highest live tree C stock, followed by mixed-species BS + TA stands and single-species BS stands.

3.2. C fluxes

Soil heterotrophic respiration was higher in single-species TA stands and mixed-species BS + TA stands than in BS stands in the QC region, while in the ON region, soil respiration was higher in single-species TA stands than in JP + BS mixtures (Table 3; Fig. 3). For a similar stand type, soil respiration was higher in the ON region than in the QC one, despite relatively similar soil MAT (Table 1). Fine root production was higher in mixed-species BS + TA stands than in single-species aspen stands in the QC region (Table 3; Fig. 3). Understory production in the ON region was higher in aspen stands than in single-species pine and mixed-species JP + BS and JP + TA + BS stands. In the QC region, understory production was marginally significant ($P < 0.10$), with TA stands having the highest value relative to other stand types. Aboveground tree production in the ON region was higher in single-species aspen and mixed-species JP + BS and TA + BS stands than in single-species pine and mixed-species JP + TA stands. In the QC region, aboveground tree production was higher in single-species aspen and mixed-species BS + TA stands than in single-species spruce stands. Comparisons of total C input (sum of fine root, understory and aboveground tree production) between stand types could not be made because fine root production was only determined for a subset of sites (19 out of 42 sites). Net mixture effects for specific C fluxes are reported in related published studies (Cavard et al., 2010; Brassard et al., 2011b; Brassard et al., 2013).

3.3. Linking total C pools and fluxes

Aboveground tree biomass was weakly to non-significantly related to understory biomass, total soil C (sum of organic layer and mineral soil C) and snag mass. Aspen basal area was strongly

Table 2

Size of the different C pools and C components (Mg C ha^{-1}) for each stand types. The dead C component includes snags, organic layer, mineral soil and dead roots. The living C component includes understory vegetation, live trees and roots. The belowground component includes organic layer, mineral soil, and dead/live roots. The aboveground component includes snags, live trees and understory vegetation. Total ecosystem C component includes all individual C pools except fine/medium roots, which were not assessed for JP + TA + BS stands in ON and for BS stands in QC. Different lowercase letters indicate a significant difference between means across stand types within a region according to the ANOVA, with "a" showing the highest mean. Degrees of freedom of ANOVAs are 5 for Ontario and 2 for Quebec.

C pool	ONTARIO												P value	QUEBEC						P value
	JP		TA		JP + TA		JP + BS		TA + BS		JP + TA + BS			BS		TA		BS + TA		
Dead aboveground																				
Snag	12.8	(3.9)	6.2	(1.9)	8.1	(1.7)	7.0	(1.0)	8.3	(2.4)	11.4	(0.4)	0.417	11.7	(3.5)	10.7	(1.9)	9.6	(0.8)	0.800
Dead belowground																				
Organic layer	21.5	(3.3)b	21.3	(1.8)b	31.2	(5.4)a	32.8	(2.4)a	36.7	(2.7)a	33.6	(0.7)a	**0.021**	37.8	(3.5)a	23.5	(1.5)c	30.2	(1.8)b	**0.001**
Mineral soil	51.4	(15.8)	61.1	(5.5)	46.4	(9.4)	45.6	(7.8)	55.5	(9.8)	97.9	(44.1)	0.435	102.7	(30.6)	93.6	(25.2)	80.6	(13.3)	0.927
Coarse root	7.9	(1.7)	3.8	(0.8)	6.5	(1.4)	5.0	(0.2)	6.7	(0.8)	5.8	(0.5)	0.216	2.3	(0.5)b	5.2	(0.8)a	3.8	(0.6)a	**0.023**
Medium root	8.4	(1.0)	11.8	(4.0)	7.5	(1.1)	4.2	(0.9)	10.9	(2.3)	n/a		0.532	n/a		8.4	(0.2)	10.1	(2.0)	0.614
Fine root	0.3	(0.0)	0.6	(0.1)	0.4	(0.1)	0.4	(0.1)	0.5	(0.1)	n/a		0.342	n/a		0.5	(0.0)	0.5	(0.0)	0.969
Living aboveground																				
Understory	3.1	(1.1)ab	9.2	(4.0)a	3.0	(1.6)ab	0.8	(0.3)b	1.2	(0.5)ab	0.7	(0.3)b	**0.050**	2.3	(0.3)a	2.0	(0.6)ab	0.8	(0.1)b	**0.019**
Tree	87.4	(10.8)	108.5	(13.3)	88.4	(6.2)	85.4	(3.0)	90.2	(8.9)	73.8	(5.2)	0.393	84.7	(4.5)c	142.5	(11.0)a	115.7	(9.0)b	**0.002**
Living belowground																				
Coarse root	25.5	(3.1)	25.6	(3.0)	25.9	(2.3)	24.0	(0.4)	23.9	(1.9)	20.2	(0.7)	0.818	17.3	(1.3)b	33.5	(2.5)a	28.7	(2.2)a	**<0.001**
Medium root	21.3	(2.4)	22.2	(3.8)	22.7	(1.9)	24.0	(3.9)	20.3	(4.5)	n/a		0.980	n/a		28.0	(3.7)	25.9	(0.3)	0.753
Fine root	1.4	(0.1)	1.5	(0.1)	1.9	(0.1)	2.0	(0.1)	2.0	(0.2)	n/a		0.111	n/a		1.4	(0.0)b	2.0	(0.1)a	**0.034**
Total dead C	100.0	(13.5)	99.9	(12.1)	98.1	(13.5)	93.5	(15.6)	114.8	(15.6)	148.7	(19.1)	0.463	154.6	(27.0)	136.3	(23.3)	128.7	(25.0)	0.829
Total living C	133.1	(13.9)	157.5	(12.4)	135.7	(13.9)	127.5	(16.0)	130.2	(16.0)	94.6	(19.6)	0.227	104.3	(13.3)c	189.1	(11.5)a	157.1	(12.3)b	**<0.001**
Total aboveground C	103.4	(9.2)	123.9	(8.3)	99.6	(9.2)	93.1	(10.7)	99.7	(10.7)	85.8	(13.1)	0.167	98.7	(10.4)b	155.2	(9.0)a	126.0	(29.7)b	**0.003**
Total belowground C	129.8	(13.4)	133.5	(12.0)	134.2	(13.4)	127.9	(15.4)	145.3	(15.4)	157.5	(18.9)	0.906	160.2	(29.0)	170.1	(25.1)	159.8	(9.6)	0.950
Total ecosystem C	209.7	(14.4)	235.8	(15.8)	209.5	(9.6)	200.6	(2.3)	222.6	(11.8)	243.3	(39.3)	0.490	258.9	(33.2)	311.0	(29.4)	269.3	(18.2)	0.349

Note: BS, black spruce; JP, jack pine; TA, trembling aspen. Numbers in parentheses are ±1 SE. *P* value in bold indicates a significant difference between means.
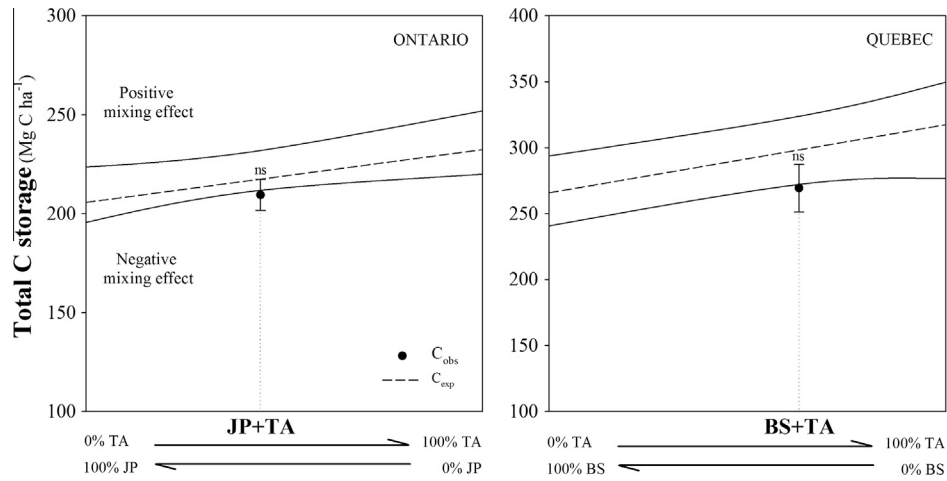
Fig. 1. Comparison of expected (C_{exp}) and observed (C_{obs}) total ecosystem C storage (±1 SE) of mixed-species stands to determine the net mixture effect for Ontario (t-value = −1.09; P = 0.357) and Quebec (t-value = −1.08; P = 0.321) sites. The dashed line represents expected total ecosystem C storage (excluding medium/fine roots) along a trembling aspen–conifer gradient derived from linear interpolation of observed C stocks from single-species stands of companion species. Net mixture effect could not be calculated for other mixed-species stands in Ontario because no single-species black spruce stands were available. Note that the average tree species proportion of total stand basal area in mixtures varies by region. ns, non-significant according to a paired t-test.
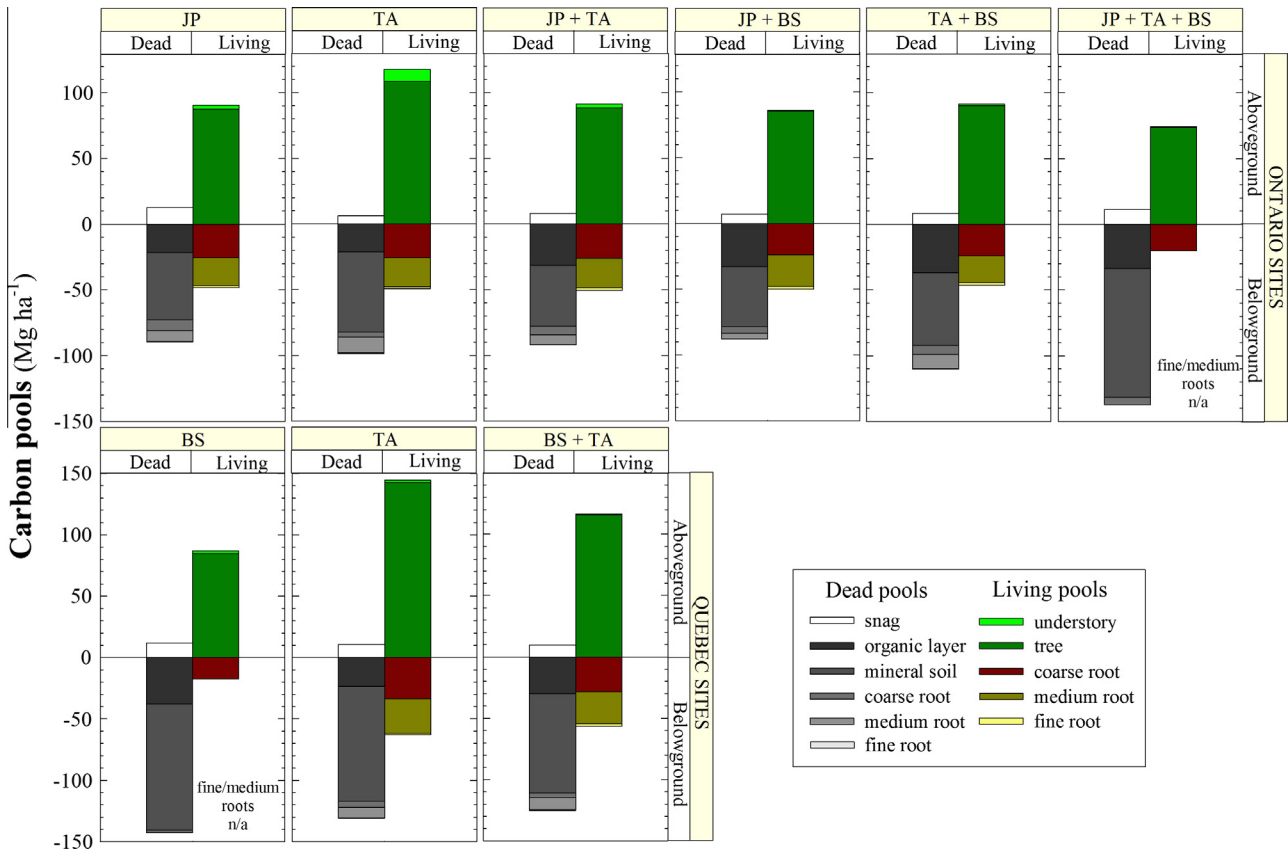
Fig. 2. Individual C pool sizes for each stand type. The different C pools are grouped into dead, living, aboveground and belowground C components (see Table 2 for significant differences among these components). Different lowercase letters indicate a significant difference between means across stand types within a region according to the ANOVA, with "a" showing the highest mean. BS, black spruce; JP, jack pine; TA, trembling aspen. Fine and medium root biomass was not assessed in JP + TA + BS and BS stands.

positively related to understory and aboveground tree biomass (Fig. 4; Table A1). Aboveground tree productivity was positively related to total C storage and weakly related to soil heterotrophic respiration (Fig. 5; Table A2). Aspen basal area was strongly positively related to aboveground tree productivity and soil respiration. The lack of pattern between mixed-species stand points (blue and green dots) and soil texture as sand proportion

in the PCAs confirms that mixed-species stands were not established on richer, finer-textured soils relative to their single-species counterparts. The apparent weak negative correlation between aspen and sand proportion in Fig. 4 is an artefact arising from a higher aspen proportion in the QC region stands, which have fine-textured soils, relative to the coarse-textured soils found in ON region stands.

Table 3
Size of the different C fluxes (Mg C ha⁻¹ year⁻¹) for each stand types. Different lowercase letters indicate a significant difference between means across stand types within a region according to the ANOVA, with "a" showing the highest mean. Degrees of freedom of ANOVAs are 5 for Ontario and 2 for Quebec.

C flux	ONTARIO														P value	QUEBEC						P value
	JP		TA		JP + TA		JP + BS		TA + BS		JP + TA + BS					BS		TA		BS + TA		
Output																						
SHR	11.4	(1.5)	15.2	(2.3)	14.3	(2.2)	8.3	(0.6)	13.7	(1.3)	11.1	(2.9)			0.242	8.1	(0.6)b	13.1	(1.0)a	12.2	(0.8)a	**0.003**
Input																						
Fine root	0.3	(0.0)	0.3	(0.1)	0.6	(0.1)	0.6	(0.1)	0.5	(0.0)	n/a				0.133	n/a		0.3	(0.0)b	0.5	(0.0)a	**0.050**
Understory	0.2	(0.2)b	1.9	(0.9)a	0.3	(0.6)ab	0.0	(0.0)b	0.2	(0.3)ab	0.0	(0.0)b			**0.038**	0.0	(0.0)	0.3	(0.2)	0.0	(0.1)	0.091
Tree	0.8	(0.1)b	1.6	(0.2)a	0.9	(0.1)b	1.5	(0.1)a	1.6	(0.2)a	1.3	(0.0)ab			**0.006**	1.1	(0.1)b	1.7	(0.1)a	1.6	(0.2)a	**0.004**

Note: BS, black spruce; JP, jack pine; TA, trembling aspen. Numbers in parentheses are ±1 SE. *P* value in bold indicates a significant difference between means.

4. Discussion

4.1. The mixed-species stands studied do not increase total C storage

Total ecosystem C storage was not higher in mixed-species stands than in single-species ones (no transgressive overyielding) and no net mixture effect was observed (no non-transgressive overyielding) in any of the regions under study. Unlike the few studies conducted in natural systems that showed mixed stands to be more productive than monospecific ones (Paquette and Messier, 2011; Vilà et al., 2013), we avoided the bias brought about by the potentially better edaphic conditions on which tree mixtures are often established by using stands that developed on similar soil conditions. However, previous studies conducted on mixed stands did detect synergistic effects of tree species mixtures on specific C pools and fluxes, such as higher organic layer C stocks (Laganière et al., 2013; Table 2) and higher fine root productivity in some mixtures (Brassard et al., 2013; Table 3), but no effects were detected on combined C pools or fluxes at the ecosystem level in the present study. The few studies that have investigated total ecosystem C storage in single-species versus mixed-species stands were mostly done in plantations of fast-growing tropical or subtropical species (e.g. Forrester et al., 2006; Wang et al., 2009; Wang et al., 2013; Wei and Blanco, 2014). Unlike our study, these studies found higher total biomass C and/or tree productivity in mixed plantations than in monocultures, while soil C was usually unresponsive to current vegetation.

Our results do not imply that the species combinations studied here may not achieve higher productivity and C storage. Our ability to observe such synergistic effects may have been limited for a
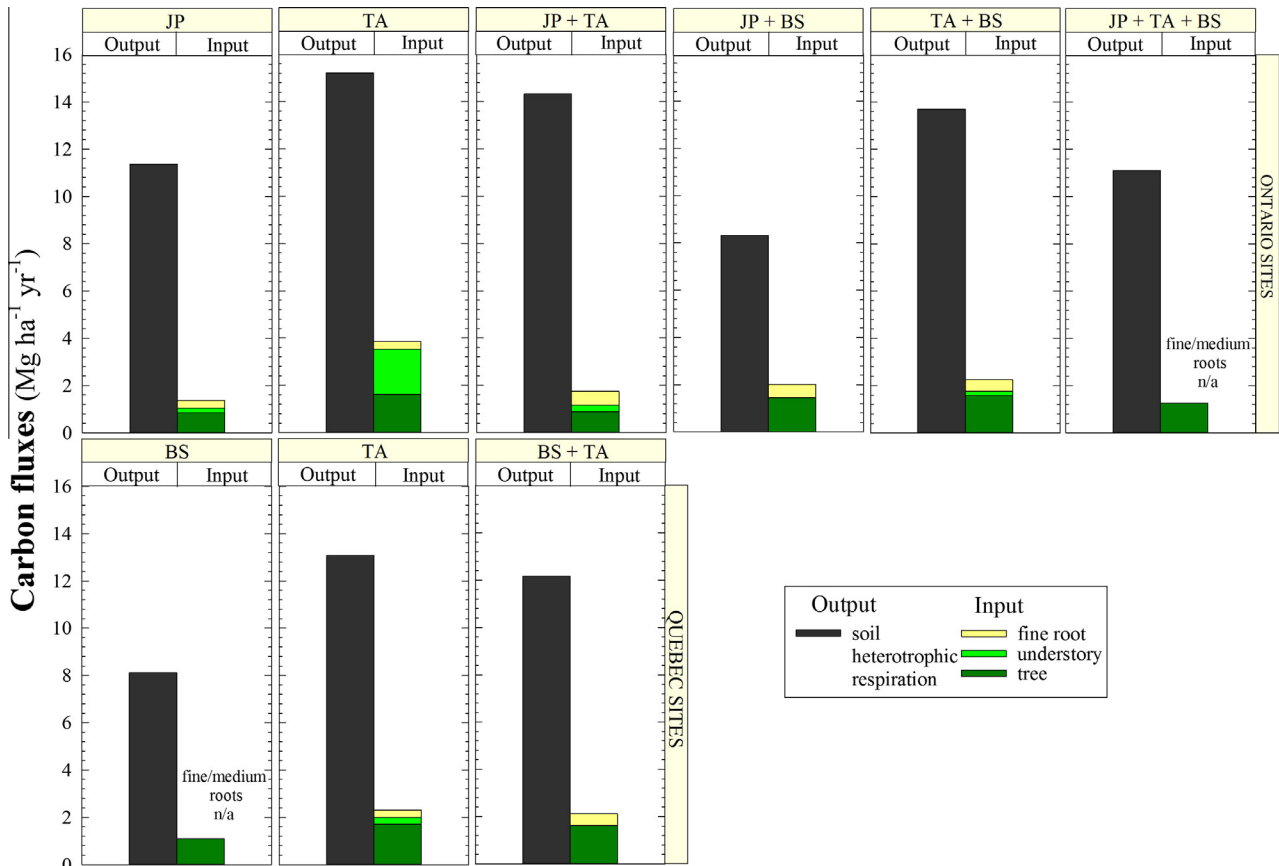
Fig. 3. C fluxes size for each stand type. Different lowercase letters indicate a significant difference between means across stand types within a region according to the ANOVA, with "a" showing the highest mean. BS, black spruce; JP, jack pine; TA, trembling aspen. Fine root production was not assessed in JP + TA + BS and BS stands.

number of reasons. First, species interactions are dynamic. It has been shown that species complementarity effects change with stand development (Binkley et al., 2003; Cavard et al., 2011b; Zhang et al., 2012; Nunes et al., 2014). For example, we may expect that a mixture effect would be more apparent during stand canopy transition, when growth rates of early successional species such as aspen or jack pine decline and those of mid- to late successional species such as spruce or balsam fir accelerate. However, early successional species remained dominant in our stands.

Second, complementarity between species may be useful only when such interactions improve the availability or the use of a limiting resource. In the QC region, for example, the parent material is a rich clay deposit with moderate drainage that may have prevented the complementary rooting pattern of black spruce (shallow) and aspen (deep) to translate into a synergistic effect because water and nutrients were perhaps not the primary factors limiting plant growth in these systems. Similarly, in the ON region, light may not have been the main limiting factor in the conifer mixture of shade-intolerant jack pine and shade-tolerant black spruce; indeed, availability of water and/or nutrients in this region's coarse-textured soils may have been more limiting. Tree diversity–productivity relationships were shown to be stronger in more stressful, northern environments where climate is harsher and resources are scarcer (Paquette and Messier, 2011; Jucker et al., 2014). In his literature review, Forrester (2014) also highlighted that complementarity effects were most often observed when resource availability was low (e.g. low N content or low water availability).

Third, all of our stands had naturally regenerated following fire and were not planted. Forrester (2014) emphasized that stand density needs to be taken into account when investigating species interactions because density may either strongly increase or decrease complementarity effects. In plantations, an optimal tree spacing that represents a trade-off between competition reduction, stem quality (shading of lower branches) and intensification of stand volume is generally promoted. In addition, when establishing a mixed-species plantation, a fine-grained mixing is generally used, in which a row of *species a* alternates with a row of *species b* or the like. In natural forests, however, tree spacing often varies greatly in space and time depending on factors such as regeneration success, edaphic conditions, competition between trees/understory vegetation, and local disturbances (Chokkalingam and White, 2001; Coomes and Allen, 2007; Gärtner et al., 2014). Ngo Bieng et al. (2013) showed that productivity in mature oak–pine stands was higher in an intimate mixture than in a patchy mixture because intraspecific competition is more severe than interspecific competition. Therefore, tree spacing and species-mixing patterns in natural forests are not controlled and may not always be optimal to favor species interactions and complementarity effects.

Fourth, synergistic effects may also depend on the proportion of species included in the mixture. In black spruce-dominated stands of western Québec, Légaré et al. (2004) found that aspen had a positive, synergistic effect on black spruce DBH and height up to a threshold of 40% of aspen basal area. Therefore, an aspen proportion higher than 40%, such as that of 60% in the present study, may have a detrimental effect on spruce growth and biomass. Furthermore, the definition of "species proportion" when assessing individual species growth in mixtures may be important as well as it may introduce wrong mixing effects (Sterba et al., 2014).

Finally, the tree species selected in the present study were not fully complementary and thus had overlapping functional traits. For example, while evergreen jack pine may avoid competition from deciduous aspen for a short period of time during the growing season (after leaves are shed in the fall until winter and in the spring prior to leafing), both species are shade-intolerant and have deep rooting patterns. Therefore, the pine–aspen complementary traits that could help minimize interspecific competition for light and soil resources may not be beneficial enough to outweigh the competition due to their overlapping traits, as observed by Longpré et al. (1994).
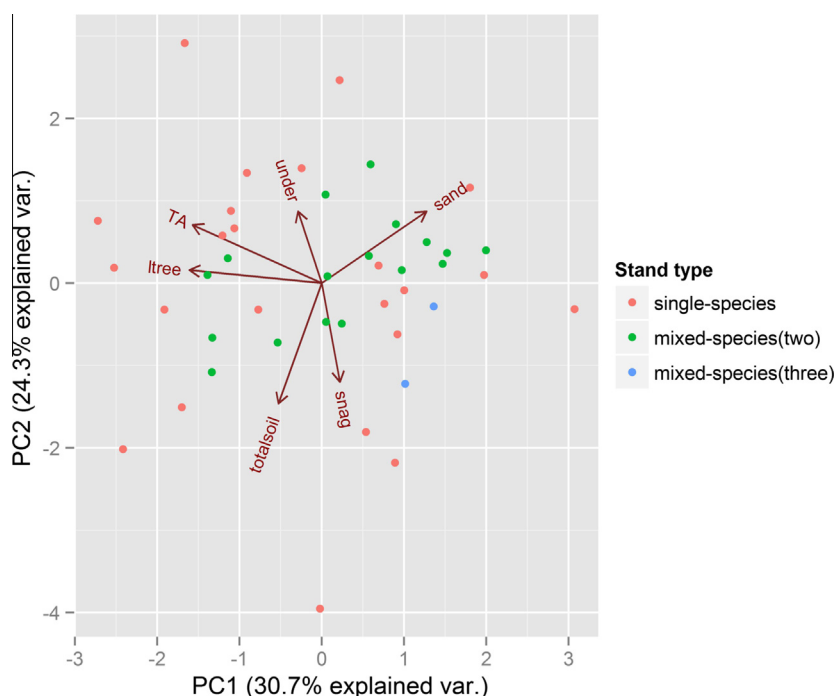
Fig. 4. Biplot of the PCA expressing the relationships between various C pools and aspen basal area. Data from both regions are included. Variables are uncorrelated when vectors are orthogonal. Variables are positively correlated when vectors go in the same direction and negatively correlated when vectors go in opposite directions. PC, principal component; ltree, living tree biomass C; sand, soil texture as sand proportion; TA, trembling aspen proportion of stand basal area; totalsoil, sum of organic layer and mineral soil C; under, understory biomass C.
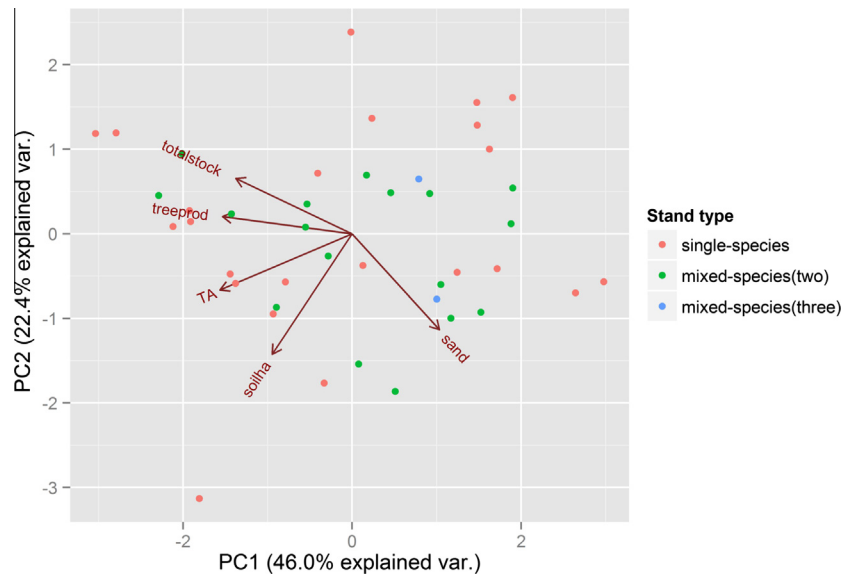
Fig. 5. Biplot of the PCA expressing the relationships between C fluxes, C storage and aspen basal area. Data from both regions are included. Variables are uncorrelated when vectors are orthogonal. Variables are positively correlated when vectors go in the same direction and negatively correlated when vectors go in opposite directions. PC, principal component; sand, soil texture as sand proportion; soilha, soil heterotrophic respiration; TA, trembling aspen proportion of stand basal area; totalstock, total ecosystem C storage; treeprod, aboveground tree productivity.

4.2. Aspen as a driver of ecosystem C storage and fluxes

While the beneficial impact of tree species mixtures on total ecosystem C stock was not apparent, aspen abundance was positively related to total C storage in both study regions due to higher aboveground tree production and tree standing stock. In fact, the highest living and aboveground C stocks were always observed in single-species aspen stands, while those of mixed-species stands were either intermediate between the two single-species stand types (QC region) or even lower (ON region). Edgar and Burk (2001) also reported higher productivity in pure aspen stands than in mixed aspen-spruce stands in northeastern Minnesota. Studies showing that aspen stands have the highest stand productivity and biomass relative to the other stand types monitored are abundant (e.g. Paré and Bergeron, 1995; Gower et al., 1997; Reich et al., 2001; Seely et al., 2002; Amiro et al., 2006).

The proportion of aspen was also positively related to soil heterotrophic respiration. Higher aboveground productivity and higher annual soil CO_2 effluxes without greater soil C storage indicate that the litter (leaf, root and branches) produced in aspen stands turns over rapidly. Aspen litter generally contains more labile compounds, nitrogen and calcium, less phenol, and has a higher pH relative to pine and spruce (Preston et al., 2000; Vance and Chapin III, 2001; Ayres et al., 2009). Micro-environmental conditions brought about by species traits and soil invertebrate communities that develop in aspen stands also promote the fast decomposition of litter materials (Ayres et al., 2009; Laganière et al., 2009; Laganière et al., 2012).

Overall, these results indicate that aspen may be considered a keystone species for determining ecosystem C storage and fluxes in these forests. Likewise, Paré and Bergeron (1995) highlighted the importance of aspen for driving aboveground biomass accumulation along a 230-year chronosequence in western Québec. They found a strong, positive relationship between aspen abundance and total aboveground biomass along the chronosequence. The high stature of aspen relative to other tree species growing in the same environment along with its low light interception in the canopy make the growth of an abundant understory vegetation possible, which may explain the large biomass aspen stands can

support (Paré and Bergeron, 1995; Hart and Chen, 2006; Bartels and Chen, 2013). These results thus support the idea that species identity/composition is a better predictor of ecosystem properties and processes, more so than species richness, as demonstrated experimentally in various systems (Hooper and Vitousek, 1997; Duarte et al., 2006; Wardle et al., 2006).

The influence of aspen on ecosystem C dynamics is not restricted to the forests of east-central Canada. Studies in other regions of North America also reported the key influence of aspen on ecosystem functions. For example, in semi-arid montane and subalpine forests of the western United States, Woldeselassie et al. (2012) found that soils from aspen forests stored greater amounts of C than soils from conifer stands. Aspen soil C stock also had higher stability against microbial decomposition, thereby potentially increasing long-term C storage relative to conifer stands. Results from Laganière et al. (2011) and Laganière et al. (2013) support these findings and further indicate that soil C storage in aspen stands is more stable against environmental changes such as climate change and human and natural disturbances. Finally, an increase in fire interval and fire severity potentially mediated by climate change could modify the successional pathway in favor of aspen stands to the detriment of jack pine and spruce species (Johnstone and Chapin III, 2006; Chen et al., 2009; Johnstone et al., 2010). Future conditions would thus promote the presence of aspen at the landscape scale, with consequent impacts on multiple ecosystem functions associated with this tree species.

5. Conclusion

Our results show that naturally-established mixtures of jack pine, black spruce and/or trembling aspen do not necessarily increase total ecosystem C storage relative to their single-species counterparts at stand maturity. We also observed that specific species composition is a key driver of ecosystem C storage and fluxes in these forests, more so than species richness. However, this does not imply that higher productivity and C storage cannot be achieved under some circumstances in mixed-species stands because species interactions vary in space and time, along with

Table A1
Loadings of PCA assessing relationships between C pools. A value higher than 0.5 is considered strong, between 0.3 and 0.5 is acceptable and under 0.3 is weak. Values below 0.1 are not shown.

	PC1	PC2	PC3	PC4	PC5	PC6
TA	−0.590	0.298		0.208	−0.302	0.649
ltree	−0.604		0.403			−0.678
under	−0.108	0.368	−0.794	0.372		−0.290
snag		−0.506	0.127	0.844		
totalsoil	−0.198	−0.617	−0.322	−0.236	−0.644	
sand	0.478	0.367	0.283	0.208	−0.698	−0.163

Note: ltree, living aboveground tree C; sand, soil texture as sand proportion; snag, snag C; TA, trembling aspen proportion of stand basal area; totalsoil, total soil C; under, understory vegetation C.

Table A2
Loadings of PCA assessing relationships between C fluxes and total C storage. A value higher than 0.5 is considered strong, between 0.3 and 0.5 is acceptable and under 0.3 is weak. Values below 0.1 are not shown.

	PC1	PC2	PC3	PC4	PC5
TA	−0.532	−0.323	0.101	0.302	0.715
totalstock	−0.468	0.319	0.137	−0.804	0.117
treeprod	−0.521		0.526	0.350	−0.565
soilha	−0.322	−0.692	−0.462	−0.224	−0.393
sand	0.351	−0.552	0.694	−0.299	

Note: sand, soil texture as sand proportion; soilha, soil heterotrophic respiration; TA, trembling aspen proportion of stand basal area; totalstock, total ecosystem C storage; treeprod, aboveground tree productivity.

light, water and nutrient availability. Species complementarity may also be effective only under some particular conditions, including specific environmental or edaphic conditions. Furthermore, when the entire forest ecosystem is considered (not only tree parts), synergistic effects of tree species mixture may be more difficult to observe because the beneficial effect of species mixing on one specific C pool may be counterbalanced by a negative effect on another pool. Finally, given the very limited literature on boreal tree species interactions, future research is needed to better identify what species-environment-climate combinations are required to obtain positive mixture-productivity relationships if mixedwood management is to be implemented in order to provide multiple desired functions and services.

Acknowledgements

Appendix A

See Tables A1 and A2.

References

Amiro, B.D., Barr, A.G., Black, T.A., Iwashita, H., Kljun, N., McCaughey, J.H., Morgenstern, K., Murayama, S., Nesic, Z., Orchansky, A.L., Saigusa, N., 2006. Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. Agric. For. Meteorol. 136, 237–251.

Ayres, E., Steltzer, H., Berg, S., Wallenstein, M.D., Simmons, B.L., Wall, D.H., 2009. Tree species traits influence soil physical, chemical, and biological properties in high elevation forests. PLoS ONE 4, e5964.

Bartels, S.F., Chen, H.Y.H., 2013. Interactions between overstorey and understorey vegetation along an overstorey compositional gradient. J. Veg. Sci. 24, 543–552.

Bennett, J.N., Andrew, B., Prescott, C.E., 2002. Vertical fine root distributions of western redcedar, western hemlock, and salal in old-growth cedar hemlock forests on northern Vancouver Island. Can. J. For. Res. 32, 1208–1216.

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, 1916–1932.

Binkley, D., Senock, R., Bird, S., Cole, T.G., 2003. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and nitrogen-fixing *Facaltaria moluccana*. For. Ecol. Manage. 182, 93–102.

Bisbee, K.E., Gower, S.T., Norman, J.M., Nordheim, E.V., 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia 129, 261–270.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Can. J. For. Res. 32, 1441–1450.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. Contribution of root respiration to soil surface CO$_2$ flux in a boreal black spruce chronosequence. Tree Physiol. 24, 1387–1395.

Brassard, B.W., Chen, H.Y.H., Wang, J.R., Duinker, P.N., 2008. Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada. Can. J. For. Res. 38, 52–62.

Brassard, B.W., Chen, H.Y.H., Bergeron, Y., Paré, D., 2011a. Coarse root biomass allometric equations for *Abies balsamea*, *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* in the boreal forest of Ontario, Canada. Biomass Bioenergy 35, 4189–4196.

Brassard, B.W., Chen, H.Y.H., Bergeron, Y., Paré, D., 2011b. Differences in fine root productivity between mixed- and single-species stands. Funct. Ecol. 25, 238–246.

Brassard, B.W., Chen, H.Y.H., Cavard, X., Laganière, J., Reich, P.B., Bergeron, Y., Paré, D., Yuan, Z., 2013. Tree species diversity increases fine root productivity through increased soil volume filling. J. Ecol. 101, 210–219.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. J. Ecol. 96, 18–34.

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

Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., 2011a. Effect of forest canopy composition on soil nutrients and dynamics of the understorey: mixed canopies serve neither vascular nor bryophyte strata. J. Veg. Sci. 22, 1105–1119.

Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., Laganière, J., Brassard, B., 2011b. Competition and facilitation between tree species change with stand development. Oikos 120, 1683–1695.

Chen, H.Y.H., Vasiliauskas, S., Kayahara, G.J., Ilisson, T., 2009. Wildfire promotes broadleaves and species mixture in boreal forest. For. Ecol. Manage. 257, 343–350.

Chokkalingam, U., White, A., 2001. Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. Plant Ecol. 156, 139–160.

Connell, K.E.B.O., Gower, S.T., Norman, J.M., 2003. Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities. Ecosystems 6, 236–247.

Coomes, D.A., Allen, R.B., 2007. Mortality and tree-size distributions in natural mixed-age forests. J. Ecol. 95, 27–40.

Duarte, S., Pascoal, C., Cassio, F., Barlocher, F., 2006. Aquatic hyphomycete diversity and identity affect leaf litter decomposition in microcosms. Oecologia 147, 658–666.

Edgar, C.B., Burk, T.E., 2001. Productivity of aspen forests in northeastern Minnesota, U.S.A., as related to stand composition and canopy structure. Can. J. For. Res. 31, 1019–1029.

Environment Canada, 2014. Canadian climate normals or averages, 1971–2000. Environment Canada, Fredericton, NB, Canada.

Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. For. Ecol. Manage. 312, 282–292.

Forrester, D.I., Bauhus, J., Cowie, A.L., 2006. Carbon allocation in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. For. Ecol. Manage. 233, 275–284.

Gärtner, S., Bokalo, M., Macdonald, S.E., Stadt, K., 2014. Variation in post-wildfire regeneration of boreal mixedwood forests: underlying factors and implications for natural disturbance-based management. New For. 45, 215–234.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., Stow, T.K., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102, 29029–29041.

Hart, S.A., Chen, H.Y.H., 2006. Understory vegetation dynamics of North American boreal forests. Crit. Rev. Plant Sci. 25, 381–397.

Hendricks, J.J., Hendrick, R.L., Wilson, C.A., Mitchell, R.J., Pecot, S.D., Guo, D., 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. J. Ecol. 94, 40–57.

Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. Science 277, 1302–1305.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Jackson, R.B., Mooney, H.A., Schulze, E.-D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sci. USA 94, 7362–7366.

Johnstone, J.F., Chapin III, F.S., 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. Ecosystems 9, 268–277.

Johnstone, J.F., Chapin III, F.S., Hollingsworth, T.N., Mack, M.C., Romanovsky, V., Turetsky, M., 2010. Fire, climate change, and forest resilience in interior Alaska. Can. J. For. Res. 40, 1302–1312.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol. Lett. 17, 1560–1569.

Kelty, M.J., 2006. The role of species mixtures in plantation forestry. For. Ecol. Manage. 233, 195–204.

Laganière, J., Paré, D., Bradley, R.L., 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., Angers, D.A., Paré, D., Bergeron, Y., Chen, H.Y.H., 2011. Black spruce soils accumulate more uncomplexed organic matter than aspen soils. Soil Sci. Soc. Am. J. 75, 1125–1132.

Laganière, J., Paré, D., Bergeron, Y., Chen, H.Y.H., 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.

Laganière, J., Paré, D., Bergeron, Y., Chen, H.H., Brassard, B., Cavard, X., 2013. Stability of soil carbon stocks varies with forest composition in the Canadian boreal biome. Ecosystems 16, 852–865.

Lal, R., 2005. Forest soils and carbon sequestration. For. Ecol. Manage. 220, 242–258.

Lambert, M.-C., Ung, C.-H., Raulier, F., 2005. Canadian national tree aboveground biomass equations. Can. J. For. Res. 35, 1996–2018.

Lamlom, S.H., Savidge, R.A., 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenergy 25, 381–388.

Légaré, S., Paré, D., Bergeron, Y., 2004. The responses of black spruce growth to an increased proportion of aspen in mixed stands. Can. J. For. Res. 34, 405–416.

Légaré, S., Paré, D., Bergeron, Y., 2005. Influence of aspen on forest floor properties in black spruce-dominated stands. Plant Soil 275, 207–220.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8, 315–323.

Longpré, M.-H., Bergeron, Y., Paré, D., Béland, M., 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). Can. J. For. Res. 24, 1846–1853.

MacPherson, D.M., Lieffers, V.J., Blenis, P.V., 2001. Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. For. Chron. 77, 351–356.

Maynard, D.G., Curran, M.P., 2007. Bulk density measurement in forest soils. In: Carter, M.R., Gregorich, E.G. (Eds.), Soil Sampling and Methods of Analysis, Second Edition. CRC Press, Boca Raton, FL, pp. 863–869.

Ngo Bieng, M., Perot, T., de Coligny, F., Goreaud, F., 2013. Spatial pattern of trees influences species productivity in a mature oak–pine mixed forest. Eur. J. For. Res. 132, 841–850.

Nunes, L., Gower, S., Monteiro, M., Lopes, D., Rego, F., 2014. Growth dynamics and productivity of pure and mixed Castanea sativa Mill. and Pseudotsuga menziesii (Mirb.) Franco plantations in northern Portugal. iForest 7, 92–102.

Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Glob. Ecol. Biogeogr. 20, 170–180.

Paré, D., Bergeron, Y., 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J. Ecol. 83, 1001–1007.

Persson, H.Å., 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil 71, 87–101.

Preston, C.M., Trofymow, J.A.Canadian Intersite Decomposition Experiment Working Group, 2000. Variability in litter quality and its relationship to litter decay in Canadian forests. Can. J. Bot. 78, 1269–1287.

Pretzsch, H., Schütze, G., 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. Eur. J. For. Res. 128, 183–204.

Reich, P.B., Bakken, P., Carlson, D., Frelich, L.E., Friedman, S.K., Grigal, D.F., 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82, 2731–2748.

Seedre, M., Taylor, A.R., Brassard, B.W., Chen, H.Y.H., Jõgiste, K., 2014. Recovery of ecosystem carbon stocks in young boreal forests: a comparison of harvesting and wildfire disturbance. Ecosystems 17, 851–863.

Seely, B., Welham, C., Kimmins, H., 2002. Carbon sequestration in a boreal forest ecosystem: results from the ecosystem simulation model, FORECAST. For. Ecol. Manage. 169, 123–135.

Senici, D., Chen, H.Y.H., Bergeron, Y., Cyr, D., 2010. Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems 13, 1227–1238.

Soil Classification Working Group, 1998. The Canadian System of Soil Classification, Third Edition. Agriculture and Agri-Food Canada, Research Branch, Publication No. 1646, Ottawa, ON.

Steele, S.J., Gower, S.T., Vogel, J.G., Norman, J.M., 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17, 577–587.

Sterba, H., del Rio, M., Brunner, A., Condes, S., 2014. Effect of species proportion definition on the evaluation of growth in pure vs. mixed stands. For. Syst. 23, 547–559.

Taylor, A., Seedre, M., Brassard, B., Chen, H.H., 2014. Decline in net ecosystem productivity following canopy transition to late-succession forests. Ecosystems 17, 778–791.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80, 1455–1474.

Vance, E.D., Chapin III, F.S., 2001. Substrate limitations to microbial activity in taiga forest floors. Soil Biol. Biochem. 33, 173–188.

Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For. Ecol. Manage. 309, 4–18.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M., Trasobares, A., 2013. Disentangling biodiversity and climatic determinants of wood production. PLoS ONE 8, e53530.

Vogel, J.G., Valentine, D.W., 2005. Small root exclusion collars provide reasonable estimates of root respiration when measured during the growing season of installation. Can. J. For. Res. 35, 2112–2117.

Wang, X.L., Klinka, K., Chen, H.Y.H., 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.

Wang, C., Bond-Lamberty, B.E.N., Gower, S.T., 2003. Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Glob. Change Biol. 9, 1066–1079.

Wang, Q., Wang, S., Zhang, J., 2009. Assessing the effects of vegetation types on carbon storage fifteen years after reforestation on a Chinese fir site. For. Ecol. Manage. 258, 1437–1441.

Wang, Q.-K., Wang, S.-L., Zhong, M.-C., 2013. Ecosystem carbon storage and soil organic carbon stability in pure and mixed stands of *Cunninghamia lanceolata* and *Michelia macclurei*. Plant Soil 370, 295–304.

Wardle, D.A., Yeates, G.W., Barker, G.M., Bonner, K.I., 2006. The influence of plant litter diversity on decomposer abundance and diversity. Soil Biol. Biochem. 38, 1052–1062.

Wei, X., Blanco, J.A., 2014. Significant increase in ecosystem C can be achieved with sustainable forest management in subtropical plantation forests. PLoS ONE 9, e89688.

Woldeselassie, M., Van Miegroet, H., Gruselle, M.-C., Hambly, N., 2012. Storage and stability of soil organic carbon in aspen and conifer forest soils of northern Utah. Soil Sci. Soc. Am. J. 76, 2230–2240.

Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J. Ecol. 100, 742–749.