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Dynamics of detrital carbon pools following harvesting of a humid eastern Canadian balsam fir boreal forest

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A R T I C L E   I N F O

A B S T R A C T

Forest management strongly influences the carbon (C) budget of boreal forests and their potential to mitigating greenhouse gas emissions. A better quantification of the net changes of carbon pools with time since harvesting is necessary to guide the development of climate-friendly forest management practices. The objective of this study was to assess the evolution of forest C pools, with a special focus on detrital biomass, in an 80-year post-harvesting chronosequence consisting of 36 very homogenous stem-only harvested plots from a humid boreal balsam fir forest of eastern Canada. Dead wood C stocks comprised of snags, stumps, downed woody debris and buried wood averaged 37 Mg C ha^{-1} and evolved according to an upward-facing «boomerang» shape pattern throughout the chronosequence (rapid decrease in the first years followed by a constant increase until the end of the time horizon). In contrast, soil C stocks (FH and mineral) averaged 156 Mg C ha^{-1} and remain constant through time. Stand C sequestration increased rapidly in the early stages up to age 50 when it reached about 250 Mg C ha^{-1}, and then continued to accumulate at a slower rate. The temporal trends observed in C pools suggest that C originating from aboveground dead wood (snags, stumps, downed woody debris) is either leaving the system (respired or leached) or transferred into buried wood, and does not appear to influence the C stocks of the fine fraction of the organic and mineral soil horizons. However, the ultimate fate of dead wood C is still poorly understood and further research is needed in this field. We recommend fixing the length of harvest rotation at a minimum of 50 years for this ecosystem to allow the build-up of its dead wood capital, and to promote dead wood retention on site. We also recommend including buried wood in carbon inventories as this pool represents an important share of the detrital C stock in these humid boreal forests.

1. Introduction

Forests and the products they generate have a strong potential to mitigate climate change (Pan et al., 2011). Forests store great amounts of carbon (C) and provide renewable sources of wood products and energy that are considered as ecological alternatives to more carbon-intensive materials (Nabuurs et al., 2007). As a result, several initiatives are taken by both scientists and practitioners to implement climate-friendly forest management and wood production practices (Schulze et al., 2000; Millar et al., 2007; Malmsheimer et al., 2011).

Maximising the potential for climate change mitigation by the forest sector relies in good part on an understanding of the forest C cycle. However, many aspects of this cycle remain poorly understood, especially the decay dynamics of downed woody debris (DWD, i.e. laying

dead wood) and C transfers to the soil or the atmosphere (Magnússon et al., 2016). Global vegetation (e.g. LPJ (Sitch et al., 2003), LM3V (Shevliakova et al., 2009)) or C dynamics models (e.g. Yasso (Rantakari et al., 2012), CBM-CFS3 (Kurz et al., 2009)) generally assume that a substantial portion of dead wood (i.e. snags, stumps, downed logs, large branches and dead roots) C is transferred to the soil organic matter reservoir (Cornwell et al., 2009). However, according to two syntheses (Nave et al., 2010; Thiffault et al., 2011a), the on-site retention of debris in the form of harvest residues (consisting of tree tops and branches) do not generally lead to significantly higher C content in the fine fraction of soil. Hence, it remains unclear to which extent dead wood contributes to soil stable organic matter formation and long-term soil C storage.

Since DWD constitute a large C pool (Laiho and Prescott, 2004;

Russell et al., 2015), contribute to maintain soil fertility (Brais et al., 2006; Zhou et al., 2007; Angers et al., 2012) enhance ecosystem biodiversity (Harmon et al., 1986; Lassauce et al., 2011), may become more abundant (Cornwell et al., 2009; Hu et al., 2017) and have their decomposition rates affected by a changing climate (Olajuyigbe et al., 2012; Pietsch et al., 2014), characterizing their C dynamics is of crucial importance to provide adequate management guidance.

Worldwide, boreal forests (1135 Mha) are estimated to contain 32% of the total forest C stocks (Pan et al., 2011). They represent a net sink of 0.5 ± 0.1 petagrams (Pg) of C year^{-1}, which compensates for about one half of the annual anthropogenic C emissions (Pan et al., 2011). Based on the categories of the International Panel on Climate Change (IPCC), forest C pools consist of aboveground biomass (i.e. all living biomass above the soil), belowground biomass (i.e. live roots), litter (i.e. non-living biomass that is not in the dead wood pool), dead wood (above- and below-ground) and soil organic matter (Penman et al., 2003). Over two decades (1990–2008), Canadian boreal forests (270 Mha) have represented a net C sink of 11 teragrams (Tg) of C year^{-1}, but there is uncertainty about the perennity of this sink due to rising temperatures and accelerated frequency of natural disturbances.

The wood decay process is a major source of C emissions in biomes with great amounts of DWD (Wu et al., 2010), which is the case in boreal ecosystems, where DWD can account for between 10% (Stinson et al., 2011) to as much as 54% (Laiho and Prescott, 2004) of the total biomass at the forest stand level. The abundance of DWD is strongly influenced by stand age and generally follows a U-shaped pattern after disturbance, which is first explained by the degradation of the trees killed by the disturbance, followed by the gradual "recruitment" of dead trees as the new stand ages (Hély et al., 2000; Harmon et al., 2011; Russell et al., 2015).

Decomposition rates are highly variable, and in moist and cold stands presenting a thick moss layer, buried wood can be abundant and remain intact for decades or even centuries (Jacobs et al., 2015; Moroni et al., 2015). Post-decay C pathways are difficult to quantify and include one or more of the following: mineralization and emission of C towards the atmosphere, dissolution and leaching in the water system, incorporation in live organisms or stabilization in soil organic matter (Cornwell et al., 2009). The fate of C from the DWD will determine the amount of C that will ultimately be transferred to the soil. The lignin-rich carbon inherited from DWD could potentially be inferred by the concentration of lignin in FH horizons, with the presence of decomposing wood and the specific microclimate conditions in the forest floor promoting the accumulation/preservation of lignin or lignin-like compounds (Strukelj et al., 2013).

The general aim of this study was to study the dynamics of the main carbon pools, and especially those of detrital biomass and soil, along a post-harvest forest rotation occurring in a humid eastern Canadian balsam fir boreal forest. Using a chronosequence approach, we pursued the following two specific objectives: (1) to assess temporal changes in the size of all forest carbon pools as defined by the IPCC (Penman et al., 2003) following stem-only clearcut harvesting, and (2) to analyse the interactions between downed woody debris and other carbon pools to determine whether a pulse of debris will later lead to any observable increases in soil organic matter pools. We hypothesized that (1) dead wood is more abundant at the beginning and the end of the rotation, (2) the temporal pattern of the soil (FH and mineral horizons) C pool does not relate to the patterns of dead wood presence and abundance; however, the temporal pattern of the buried wood C pool follows that of dead wood and (3) the composition of the organic matter in the FH horizons does not show any chemical enrichment from decay of debris, that is, its lignin concentration will not vary significantly through time or in accordance with the dead wood accumulation curve.

2. Material and methods

2.1. Study site

The Forêt Montmorency (47°19′19.6″N 71°08′49.6″W), the research forest of Laval University (Quebec, Canada), covers 412 km^2 in the southeastern portion of the Canadian boreal forest. It is located within the balsam fir - white birch bioclimatic domain and is characterized by a cold and moist climate. Mean annual temperature and precipitation are 0.5° and 1583 mm (964 mm in rain and 620 mm in snow) (Environment and Climate Change Canada, 2017). The natural disturbances shaping this forest landscape are recurrent spruce budworm outbreaks (with intervals of 30–40 years) and windthrows, the significant pluviometry limiting wildfires. The main soil type is ferro-humic podzol, with relatively frequent seepage. Historically, the Forêt Montmorency was covered by a fine heterogeneous mosaic of mostly mature and irregular stands of balsam fir companioned by white birch, white spruce and, less commonly, black spruce and trembling aspen. Although partial cuts are gaining importance in the Forêt Montmorency's management strategy, the main harvest type is clearcut harvesting with protection of advance regeneration and soils.

2.2. Experiment design

Data were collected from a chronosequence of forest stands of various ages located within Forêt Montmorency, all originating from clearcut, stem-only harvesting (i.e. tree tops and branches were left on site). The chronosequence consisted of 36 plots ranging from 1 to 80 years after harvest. They showed nearly identical ecological and geomorphological properties (parent material, soil granulometry, slope, aspect, altitude and drainage) based on mapping info and site evaluation (see Appendix A for ecological and geomorphological information). All plots were classified as belonging to the same ecological type according to Quebec classification (MS22: Balsam fir-white birch stand on shallow to deep deposits, with medium drainage and medium soil texture) (Ministère des Ressources naturelles de la Faune et des Parcs, 2004), and had site index ranging from 13.5 to 15 m at age 50.

2.3. Data collection

The protocol for data collection was inspired by the guidelines for ground plots of Canada's National Forest Inventory (NFI) (National Forest Inventory, 2008) and by the protocol of Thiffault et al. (2011b). Each plot of the chronosequence was circular in shape with a 20-m radius (area of 1250 m^2). At the center of the main plot, two smaller circular inventory plots of a 11.28-m (400 m^2) and 3.99-m radius (50 m^2) were installed to measure large vegetation and snags, and small vegetation and stumps, respectively. In addition, two 20 m-long perpendicular transects intersected at the center of the main plot were established for woody debris inventory. Soil was sampled in 6 stations positioned within the boundary of the main plot.

2.3.1. Downed woody debris

On the two perpendicular 20-m long transects, every piece of laying dead wood of more than 1 cm in diameter crossing the transect (i.e. laying on the ground or suspended above it) was counted and its decay class was categorised (from Class 1: Intact and hard, to Class 5: Totally decomposed and soft; National Forest Inventory (2008)). The diameter of each woody debris was measured using a calliper held perpendicular to the debris at the point where it intersected the transect. DWD were divided in two size categories: 1.1–3 cm and > 3 cm in diameter, which correspond, respectively, to small and coarse DWD. Debris ≤ 1 cm or

less in diameter were categorized as fine DWD and were accounted for in the soil sampling. The two perpendicular transects were 10 m long on both sides of the center of the main plot. The inventory of the small DWD was made along the first and last 5 m of each transect line (four 5-m sections in total), whereas the coarse DWD were inventoried along the full length of the transects (i.e. 40 m in total).

2.3.2. Large trees and snags

In the 11.28 m radius plot, trees and snags with height of more than 1.3 m and a diameter at breast height (DBH) over 9 cm were tallied and measured. The DBH was determined for every tree or snag, whereas height was determined only for three live trees and three snags randomly sampled among the dominant/co-dominant stems of the stand. Snags shorter than 1.3 m or overturned were respectively classified as stumps and DWD.

2.3.3. Stumps

In the 3.99 m radius plot, the height, width, diameter and decay class of each stump were recorded. The diameter was measured with a calliper pointing towards the center of the plot. The height was measured from the highest ground point.

2.3.4. Understory vegetation

The biomass/carbon content was not measured. However, to provide an estimate of carbon pools associated with understory vegetation, five ground plots from the NFI network located within Canadian boreal stands of various ages and having similar vegetation composition were selected. In these plots, all understory vegetation was clipped from four 1-m^2 quadrats, before being dried in oven (until constant mass) and wheighted. These plots provide an estimate of carbon stocks in the understory vegetation of about 1.5 Mg C ha^{-1}.

2.3.5. Soil

In each stand, the soil was sampled volumetrically at 6 stations. Fine woody debris (< 1 cm in diameter), L horizon and FH horizons were collected using a 20 × 20 cm template. Contrary to the IPCC definition of the litter pool, in our case the L horizon mostly consisted of live mosses. The depth of the L horizon layer and the FH horizons was recorded in the field. The mineral soil was sampled sequentially at 3 depths (0–15 cm, 15–35 cm and 35–55 cm) using metal tubes with an internal diameter of 5 cm. In all cases, roots were kept when present in the samples.

2.4. Laboratory analyses and computations

2.4.1. Carbon quantification

FH horizons and mineral soil samples were air dried and respectively sieved with 4 mm and 2 mm screens. The coarse portion that did not pass through the screens was separated into fractions: rock, root, buried wood and other organic material. Fine material that passed through screens and coarse portions were both oven-dried at 55° during 2 days and weighed. Soil C concentration (%) was determined on the fine soil fraction by dry combustion using a Leco TruMac CNSanalyzer (Leco Corp., St. Joseph, MI, USA). The bulk density (g cm^{-3}) of the FH horizons was calculated from the mass of the samples, the area of the sampling template and the depths of the horizons, whereas mineral soil bulk density (g cm^{-3}) was calculated on the fine fraction using volumetric cores and mass of the samples.

The biomass of trees and snags was obtained using DBH-based allometric equations of Lambert et al. (2005), while the biomass of stumps and woody debris was obtained using equations from Canada's National Forest Inventory based on volume (via dbh and transect length) and density (oven-dry mass to saturated wood volume coefficients for each decay class and species). The C content (in Mg ha^{-1}) of live trees and snags was determined by multiplying their biomass (Mg ha^{-1}) by 0.5, a commonly applied method for converting biomass

Table 1
Carbon concentration (%) of various types of material. Average and standard deviation of 3 samples.

Material	% C
Woody debris per decay class	
Class 1	49.83 ± 7.58
Class 2	50.32 ± 5.95
Class 3	49.94 ± 10.07
Class 4	49.22 ± 8.17
Class 5	50.02 ± 7.35
Mosses	42.59 ± 8.97
Leaf and needle litter	51.80 ± 8.41

into C concentration (Penman et al., 2003). To validate the 0.5 value, three samples of debris from the different decay classes, along with three samples of live mosses, dry needles and leaves were collected and analysed for carbon concentration using a LECO CNS-2000 analyzer. Results (Table 1) were all very close to 0.5, with no obvious difference between types of material or decay classes.

The carbon content in Mg of C ha^{-1} of the L and FH horizons, as well as the mineral horizons (to a 55-cm depth), was determined by adjusting LECO assessments with bulk densities, and converting sampling units of measure into Mg of C per hectare. The C content of the FH and mineral horizons therefore correspond to the carbon in the fine soil fraction.

2.4.2. Acid detergent lignin quantification

Gross acid detergent lignin concentration (%) (corresponding to the acid-unhydrolyzable residue) of the fine fraction of FH horizons (n = 108) was determined using an ANKOM^{200} fiber analyser (ANKOM Technology, Macedon, NY, USA), by first performing acid detergent fibre analysis (with 20 g cetyl trimethylammonium bromide to 1 L 1.00N H_2SO_4), followed by acid detergent lignin analysis (with H_2SO_4 24N). Net acid detergent lignin concentrations (%) were obtained by adjusting ANKOM assessments with dry matter correction (g) and ash content (g) determined by dry combustion of samples in an oven.

2.5. Statistical analysis

All statistical analyses were conducted with JMP® Pro version 12.0.1 (SAS, Marlow, Buckinghamshire, UK) using a confidence level of 95% (α = 0.05) and data from all plots (n = 36). To describe evolution of C pool sizes through time, i.e. accumulation pattern of C in each pool after harvest, statistical model fit curves were produced using linear and nonlinear regressions of C content for individual and grouped pools as functions of stand age. The model for the live trees and tree foliage pools were based on the Chapman-Richards equation, which is a commonly used model to describe forest growth (Pienaar and Turnbull, 1973). For other pools, the raw data was plotted and various linear and nonlinear model forms were chosen to represent the observed patterns of variation over time, including a customised nonlinear model proposed by Barrette et al. (2013). Model selection was based firstly on a visual appreciation of their aptitude to represent the observed patterns. Then, a choice was made among potentially applicable model forms based on goodness-of-fit, assessed through the r-squared value (or pseudo r-squared in the case of nonlinear models, calculated as the coefficient of determination of a regression fitted between predicted and observed values).

Chi-square analyses were performed to assess the variation in the proportions of different detrital biomass C pools (i.e. buried wood, FH horizons, DWD, snags and stumps) among stand age classes. Although L horizon is normally considered as detrital biomass, we considered it as live biomass in this study because our L horizon samples consisted mostly of live feathermosses) instead of dead litterfall. Stand age classes were chosen according to the successional stages defined by the NFI,

Table 2

Statistical models, predictive model formulas, p values, r^2 and mean fit values of carbon pools as a function of stand age (in Mg of C/ha). See Figs. 1 and 3 for corresponding graphs.

Carbon pools	Model	Predictive formula	p	r^2
Live trees[1] (Fig. 1a)	Chapman-Richards	$77.124*[1-e(-0.043*AGE)]^{3.294}$	< 0.0001	0.88
Tree foliage (Fig. 1b)	Chapman-Richards	$15.022*[1-e(-0.017*AGE)]^{1.478}$	< 0.0001	0.95
L horizon (live mosses) (Fig. 1c)	Biexponential 4P	$2.382*e^{(0.006*AGE)} + 4.922*e^{(-0.157*AGE)}$	< 0.0001	0.64
Roots (live) (Fig. 1d)	Lorentzian peak	$\frac{(11.669*32.394^2)}{[(AGE-24.993)^2 + 32.394^2]}$	0.0001	0.49
Total live biomass[2] (Fig. 1e)	Gompertz 3P	$94.947*e\{-e[-0.039*(AGE-23.08)]\}$	< 0.0001	0.85
Downed woody debris (Fig. 1f)	Biexponential 4P	$4.12*e^{(0.007*AGE)} + 19.988*e^{(-0.108*AGE)}$	< 0.0001	0.80
Stumps (Fig. 1g and h)	Exponential 2P	$1.096*e(-0.017*AGE)$	< 0.0001	0.47
	Quadratic	$0.879-0.009*AGE + 0.0002*(AGE-40.765)^2$	< 0.0001	0.47
Snags (Fig. i)	Gompertz 3P	$11.273*e\{-e[-0.02*(AGE-46.154)]\}$	< 0.0001	0.55
Total aboveground dead wood[3] (Fig. 1j)	Biexponential 4P	$5.555*e^{(0.013*AGE)} + 23.514*e^{(-0.152*AGE)}$	< 0.0001	0.71
FH horizons (Fig. 1k)	Simple linear regression	$31.342-0.015*AGE$	0.8047	0.00
Buried wood ((Fig. 1l)	Customised nonlinear regression	$e^{(-0.144*AGE)}*17.503 + 0.125*AGE$	< 0.0001	0.81
Total belowground detrital biomass[4] (Fig. 1m)	Customised nonlinear regression	$e^{(-0.034*AGE)}*44.723 + 0.574*AGE$	0.0103	0.24
Total detrital biomass[5] (Fig. 1n)	Simple linear regression	$34.735-0.230*AGE$	0.0204	0.15
Mineral soil[6] (Fig. 1o)	Simple linear regression	$107.607 + 0.404*AGE$	0.1697	0.07
Total ecosystem (Fig. 3)	Biexponential 4P	$182.792*e^{(0.006*AGE)}-179.472*e^{(-0.186*AGE)}$	< 0.0001	0.90
	Exponential 3P	$267.396-241.721*e^{(-0.064*AGE)}$	< 0.0001	0.87

[1] Stem, bark and branches.
[2] Trees, foliage, L horizon and roots.
[3] Snags, stumps and DWD.
[4] Buried wood and FH horizons.
[5] FH horizons, buried wood, DWD, stumps and snags.
[6] To a 55-cm depth.

that is, early seral stage (0–20 years), mid-seral stage (20–30 years), late seral stage (40–60 years) and mature seral stage (60–80 years) (National Forest Inventory, 2008). Finally, the evolution pattern of lignin concentration in the FH horizons was described by fitting a nonlinear regression with FH horizons ADL content as a function of stand age. The criteria of homogeneity of variances and normality of residues were tested and were met for all statistical analyses, except for live trees and total live biomass regressions, for which residues showed minor heteroscedasticity. No data transformation was performed.

3. Results

3.1. Evolution of C stocks

Regression curves of C stocks as a function of stand age were all statistically significant except for the mineral soil and FH horizons, which showed non significant variation of C contents with stand age (Table 2; Fig. 1). The evolution of each C pool through time was described by nine different types of functions, the most common being the four-parameter biexponential describing the L horizon, DWD and total ecosystem pools, the Chapman-Richards describing live trees and foliage, the three-parameter Gompertz describing total live biomass and snags, and finally a customised nonlinear regression (Barrette et al., 2013) describing buried wood and total belowground detrital biomass (Table 2; Fig. 1).

The total aboveground detrital biomass followed a four-parameter biexponential model, while two of its separate compartments (snags and stumps) followed different ones (Table 2). Although FH horizons and mineral soil C contents showed no significant trends through time, a significant relationship between C stock and stand age was found for belowground detrital biomass, which followed the same nonlinear model as for buried wood, the latter being highly significant (Table 2).

The four-parameter biexponential and customised nonlinear models, despite their distinctive equations, produced very similar fit curves, somewhat similar to a boomerang shape, showing a steep initial decrease followed by a more or less abrupt increase depending on the pool. The curves displayed minimum values between age 20 and 30 (Fig. 1c, f, l and m). Among the pools following such a pattern, the strongest and weakest increases were respectively observed for buried wood and DWD.

The three-parameter Gompertz and Chapman-Richards models also both produced similar fit curves with slightly sigmoïdal increases, this shape being more obviously depicted by live tree parts (Fig. 1a, b). For all curves following one or the other of these two models, two inflexion points could be seen at about years 15 and 55.

Generally, pools of C in live biomass showed constantly increasing pattern (Fig. 2a), while pools of dead wood (buried wood, DWD, stumps and snags) followed the boomerang pattern (Fig. 2b). Soil C pools (FH and mineral horizons) remained rather constant (non statistically significant relationship with time; Table 2).

Total ecosystem C could be described by either one of two statistical models showing nearly identical p values and r^2 (Table 2); the two models can thus not be discriminated based on probability value or goodness-of-fit. In comparison to the three-parameter exponential model, the four-parameter biexponential model predicted less C accumulation between 20 and 60 years, and more C accumulation after 60 years (Fig. 3).

Overall, both models described a gradually decreasing C accumulation rate (slope of the curve) with stand age (Fig. 3). With the three-parameter exponential, this accumulation rate gradually slowed down until C accumulation became almost null around age 50: the curve described a near linear increase in biomass until age 25, which started to level off at about age 40, and tended towards an asymptote beyond age 50 (Fig. 3). With the four-parameter biexponential model, the rate of C accumulation slowed down sharply at around age 20, and then stayed more or less constant until age 50 before increasing again for the rest of the rotation. In summary, the four-parameter biexponential model predicted that the ecosystem would keep sequestering C after year 50, whereas the three-parameter exponential model predicted that ecosystem C stocks would stay almost constant after that time. Regardless of the fitted models, the dispersion of the observations on the plot (each point representing a field plot) showed a linear, tight accumulation pattern from age 0 to 25, while there was more variability among plots from age 25 to 45.
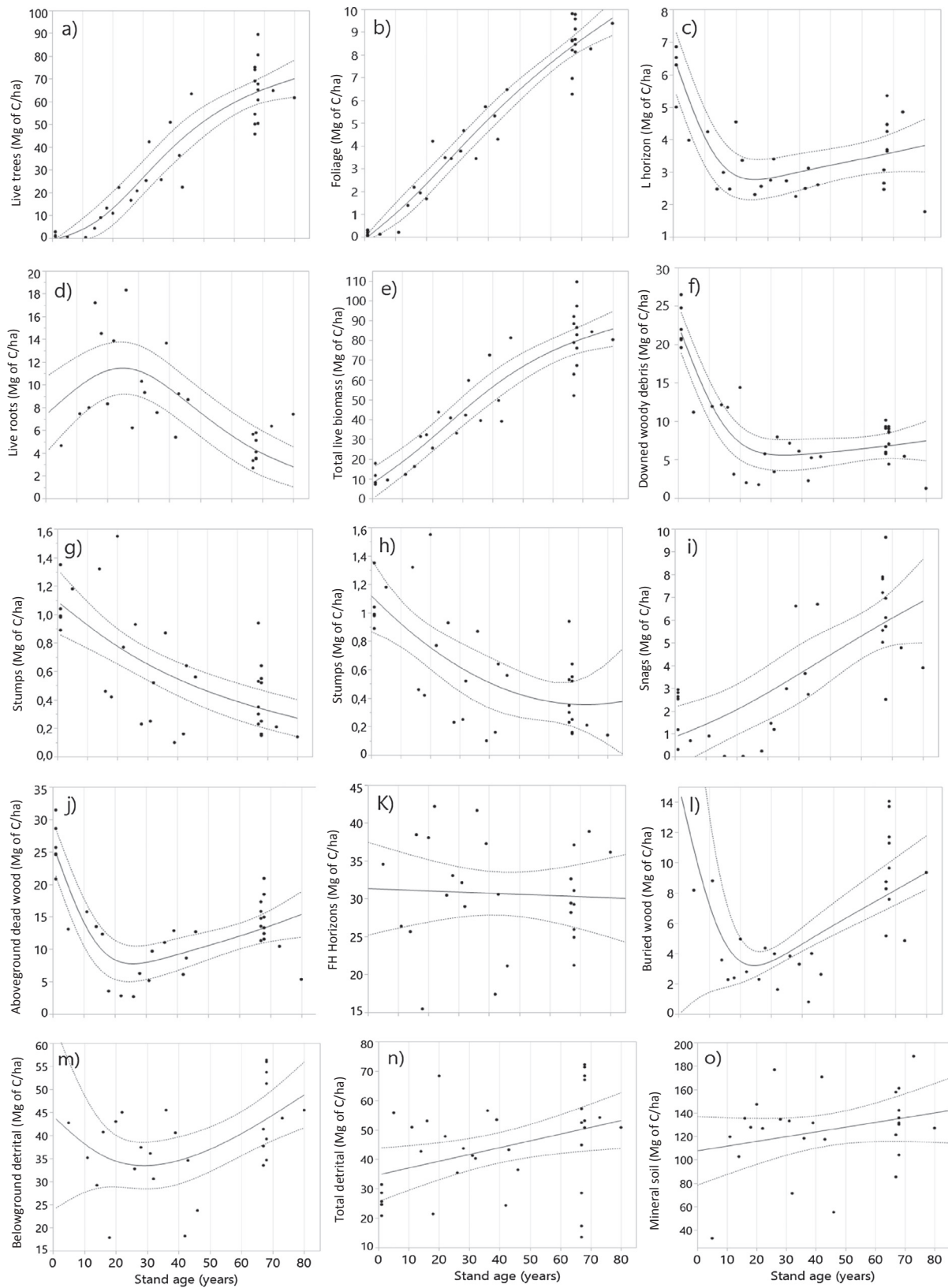
Fig. 1. Predictive models of carbon pools as a function of stand age. See Table 2 for corresponding formula and definitions of pools. All models are statistically significant at p = 0.05, except for graphs (k) (FH horizons) and (o) (mineral soil).
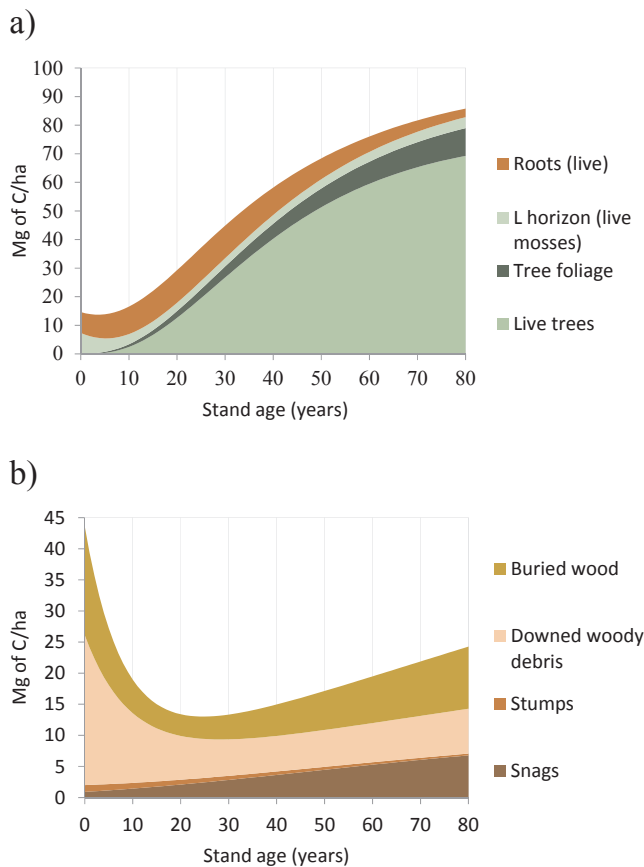
a)

b)

Fig. 2. Superposition of (a) live biomass, and (b) detrital biomass according to stand age. See Table 2 for predictive models.
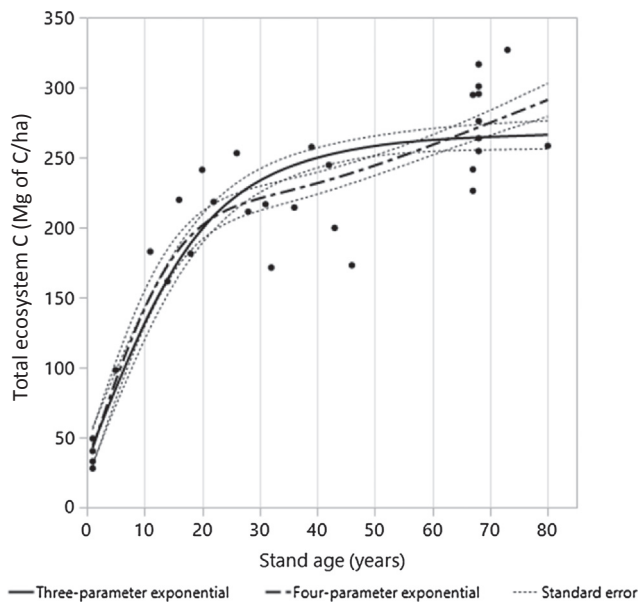

Fig. 3. Predictive models of total ecosystem C as a function of stand age.

3.1.1. Variation of relative C proportions in detrital biomass pools

A significant effect of stand age was found on the C distribution within pools of detrital organic C, i.e. DWD, snags and stumps, buried wood and FH horizons, excluding mineral soil (χ^2 (9, N = 197) = 21.087, p = 0.0123). Overall, the FH horizons always contained the largest proportion of C (Table 3). Up to 40 years, the DWD fraction was the second most important pool. Gradually its

importance shifted to the snag and stump pool at age 40–60, and finally, at the 60–80 year stage, buried wood became the second largest pool, after FH.

3.1.2. Chemical signature of wood decay in FH horizons

The model found to best describe the relationship between acid detergent lignin content of the FH horizons and stand age also used a four-parameter biexponential that fitted a boomerang curve (Fig. 4). The amount of lignin in FH horizons followed the same predictive model as the other pools of dead wood (Fig. 2b), but the inflexion point occurred a little later, i.e. shortly after 30 years (Fig. 4).

4. Discussion

This chronosequence-based study made it possible to assess the carbon dynamics following harvesting of a humid boreal forest dominated by balsam fir. Although the downsides of the chronosequence approach are well known (Yanai et al., 2003a; Johnson and Miyanishi, 2008), its inherent benefits (e.g. time for space substitution) and demonstrated potential for assessment of ecological processes (Foster and Tilman, 2000; Walker et al., 2010; Phillips, 2015), may warrant its use. In our case, the chronosequence approach yielded a series of models that can be used to pred the evolution of carbon pools throughout a harvest rotation in boreal stands. The relatively high goodness-of-fit of the models was probably due in part to the very homogeneous edaphic conditions among sample plots, as well as to the absence of change in logging methods through time.

4.1. Carbon stocks

Above- and below-ground carbon stocks predicted by our models for Forêt Montmorency are in the range of values of those estimated by Beaudoin et al. (2014) (average for Boreal Shield: 30 Mg C ha^{-1} for aboveground biomass) and Tremblay et al. (2002) (fir stands: 16–118 Mg C ha^{-1} for FH horizons, 2–279 Mg C ha^{-1} for mineral horizons up to 70 cm in depth) for boreal forests of Quebec. Although carbon stocks in understory vegetation were not measured directly in the chronosequence plots, estimates from similar boreal plots of the NFI network suggest that understory vegetation represents about 1.5 Mg of C ha^{-1} (National Forest Inventory, 2008), i.e. from 0.6 to 3% of the total carbon stocks of a forest stand.

The values and the trends through time also show great similarities with the observations of Sprugel (1985) for wave-regenerated balsam fir forests. Detrital biomass C in the form of aboveground dead wood (i.e. snags, stumps and DWD) and buried wood C formed two peaks, one at the very beginning of the rotation, and another one, albeit less sharp, at the end of the rotation. These empirical observations were consistent with the literature, which states that dead wood biomass accumulation in boreal forests generally follows a «U» shape pattern (Hély et al., 2000; Harper et al., 2005; Seedre et al., 2011; Russell et al., 2015), somewhat similar to the boomerang shape we observed. In our case, the first peak was induced by logging residues (tree branches and tops left on site), and by residual stumps and snags that are run over and brought down by harvesting machinery, while the second peak was caused by natural tree senescence. The fact that the shape of our curve resembles a boomerang rather than the more usual «U» shape is caused by a somewhat slower accumulation of detrital biomass in the second half of the rotation, relative to the sharp decrease observed in the first decades.

For detrital biomass pools, whether individual or combined, the lowest C stocks were observed at the beginning of the mid-seral succession stage (i.e. between year 20 and 30). However, C stocks in the FH horizons (also considered as detrital biomass) stayed more or less constant throughout the rotation, similarly to mineral horizon C. An inversely proportional relationship between the bulk density of the FH horizons and their C content (Fig. 5) led to a flat accumulation curve. While the literature generally reports no change in mineral soil C stocks

Table 3

Proportions of C (%) in detrital biomass carbon pools according to stand age classes (years).

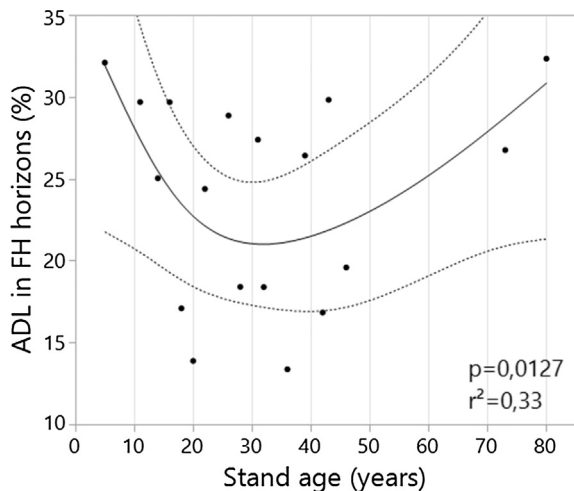|	Downed woody debris	Snags and stumps	Buried wood	FH horizons
0–20 yrs	31.73 (12.89)	5.59 (3.93)	9.53 (5.40)	53.15 (15.08)
20–40 yrs	12.48 (7.83)	7.76 (7.65)	6.96 (2.13)	72.80 (9.68)
40–60 yrs	12.46 (4.17)	13.91 (5.49)	7.16 (3.78)	66.47 (16.01)
60–80 yrs	12.07 (3.95)	12.88 (6.53)	24.08 (13.67)	50.97 (8.70)
Average	17.31 (12.17)	9.75 (8.52)	15.02 (14.06)	57.09 (12.81)

Fig. 4. Predictive model of acid detergent lignin (ADL) in FH horizons as a function of stand age.

Fig. 5. Predictive models of (a) bulk density and (b) carbon concentration of FH horizons as a function of stand age.

with time since the last disturbance (Johnson and Curtis, 2001; Martin et al., 2005; Deluca and Boisvenue, 2012; Kurz et al., 2013), organic soil horizons C stocks can be more variable with stand age (Pregitzer and Euskirchen, 2004; Jandl et al., 2007; Seedre et al., 2011). However, Yanai et al. (2000) suggested that many artefacts such as mixing of the organic layer with the mineral soil by logging equipment, or changes in density within this layer, have lead to potential overestimation of C losses in the FH horizons over time.

The accumulation curve of root C found in this study is not consistent with the literature: biomass of fine roots should be constantly increasing over time (Yuan and Chen, 2010; Makkonen et al., 2012), and that of coarse roots should be proportional to the biomass of live trees (Bond-Lamberty et al., 2002; Mokany et al., 2006). This difference is likely caused by soil sampling procedures and treatment. Because most fine roots probably passed through sieves, they could have been included in the soil pool rather than in the roots pool. Also, the amount of coarse roots was certainly underestimated since soil sampling was preferentially performed in spots with no important physical barriers to the passage of the metal tubes (e.g. rocks or coarse roots).

We could not statistically discriminate between the two models that predicted contrasted accumulation patterns of total forest ecosystem C towards the end of the rotation. The low number of plots representing older stands (> 50 years old) and the large variability among plots starting from age 25 likely explain the statistical difficulty of choosing a model. Between the two tested models, the three-parameter exponential was the most consistent with the literature (Mund et al., 2002; Pregitzer and Euskirchen, 2004; Goulden et al., 2011) and, ecologically speaking, the most plausible one. The four-parameter biexponential model was indeed predicting rapid C sequestration and high C stocks in the long term (i.e. 80 years and over) (Kurz et al., 2013), contrarily to the negligible increase predicted by the three-parameter exponential after age
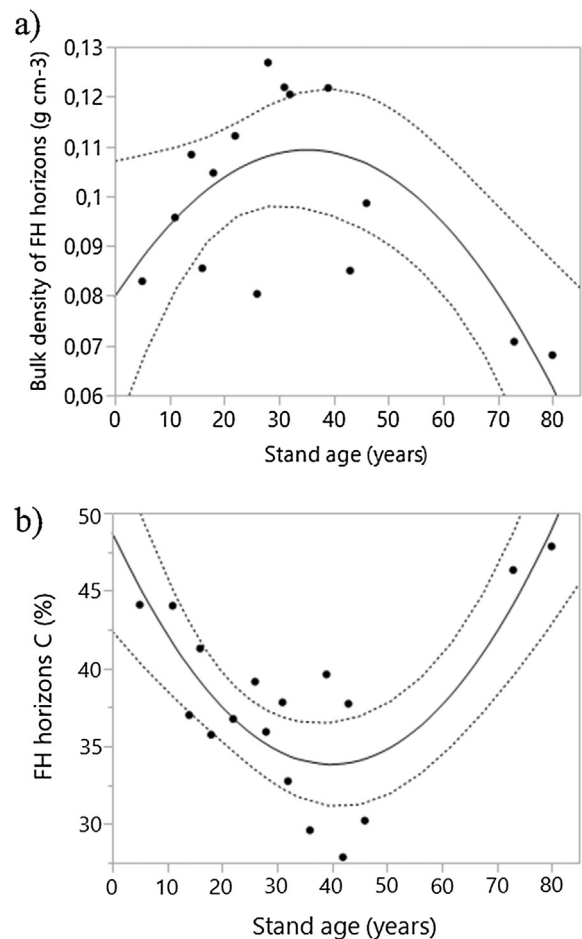
50. Although there is a consensus about the decline of net carbon uptake with age (Magnani et al., 2000; Binkley et al., 2002; Ryan et al., 2004), there is more inconsistent information regarding the carbon balance of overmature or old-growth forests (Luyssaert et al., 2007; Harmon et al., 2011). There is evidence in the literature that some forest ecosystems may continue to sequester C in their late succession stages, albeit at a very slow rate that is close to neutrality (Carey et al., 2001; Litvak et al., 2003; Luyssaert et al., 2008). Based on the dispersion of the points, our results showed an increasing variability of C sequestration with stand age. This may be attributable to the increased probability of occurrence of minor/localized natural disturbances as stands get older, such as partial mortality caused by tree windthrow or spruce budworm defoliation (mature balsam fir being susceptible to both) (MacLean, 1984; Achim et al., 2005). Such disturbances reduce growing tree stocks and create pulses of downed woody debris in stands. Future research should aim to make similar measurements in older balsam fir forests to provide better assessments of the potential trajectories of the total forest ecosystem C curve in mature/overmature stands.

4.2. Carbon partitioning among detrital pools

We found that FH horizons, DWD, buried wood and standing dead wood (snags and stumps) were contributing to 60%, 17%, 13% and 10% of detrital biomass C stocks (excluding the mineral soil), respectively. The large variability of carbon pool assemblages found in the literature makes the validation of such results quite complex. Our results showed that the studied forest ecosystem contains substantial

amounts of buried wood, which stored on average more C than standing dead wood, particularly in the mature (i.e. 60–80 years) successional stage. Buried wood stocks are often overlooked, but have been found to be larger than standing dead or aboveground downed dead wood stocks in boreal forests (Moroni et al., 2015). This is especially the case where ecological conditions are favorable to wood burial, i.e. high moisture level, low temperature and bryophyte ground vegetation, which are conditions observed in our study area.

4.3. Carbon transfers among pools

Results did not reveal any obvious relationships between DWD and the soil C pool. On the other hand, the observed curves suggest that DWD enrich the buried wood C pool. A portion of DWD is also presumably respired to the atmosphere and (likely, marginally), leached through soil and to water courses as dissolved organic carbon.

Regardless of the quantity of DWD present on site, the total amount of organic C in the fine soil fraction (excluding live mosses, recognizable woody debris and roots) remained constant throughout the chronosequence. Nonetheless, there is still a portion of recalcitrant C (as expressed by the measured concentrations of acid detergent lignin), likely resulting from decay of lignin-rich material, that is somehow transferred into the fine fraction of soil. The acid detergent lignin accumulation curve followed more or less that of the DWD and buried wood curves. The large variability of carbon stock data observed in soil horizons (partly a consequence of working with a chronosequence) might also limit the likelihood of detecting a significant trend through time; as described by Yanai et al. (2003b), most studies on soil carbon fail to detect changes that are smaller than 15–20%.

The DWD pool showed a decrease of about $16 \pm 2\, \mathrm{Mg\, C\, ha^{-1}}$ in the early stages of the chronosequence, the lowest point of the curve being reached around year 40. The buried wood pool also decreased until year 20 by about $14\, \mathrm{Mg\, ha^{-1}}$, and then showed a relatively sharp increase of about $6 \pm 1.5\, \mathrm{Mg\, C\, ha^{-1}}$ until the end of the rotation. These visual observations suggest that some amounts of C are transferred from DWD to buried wood, at least from year 20. It is possible that buried wood is also partially decomposed and incorporated to the fine fraction of soil (contributing to the acid detergent lignin that we measured). But again, given the stability of soil C through the stand rotation, it is possible that a major part of DWD and buried wood is eventually respired to the atmosphere and, marginally, leached towards the water system. Nevertheless, the ultimate fate and importance of this C to soil stable organic matter remains unclear (Magnússon et al., 2016).

The residence time of buried wood can range from decades to centuries (Moroni et al., 2015). To consider buried wood as stable organic matter or not is, *inter alia*, a question of time scale. Our results showed an accumulation of buried wood in the second half of the chronosequence, meaning that the residence time of buried wood may exceed the rotation length. This is consistent with the fact that in cold and moist environments such as the Forêt Montmorency, decomposition can be very slow and buried wood can remain intact for a long time (Hagemann et al., 2009; Hagemann et al., 2010). Nevertheless, this may also be observed in the drier, fire-driven boreal forests generally found in North America, as pyrogenic wood (i.e. char) is very resistant to decomposition due to its high lignin content (Preston and Schmidt, 2006; Knicker, 2011). Given the high abundance and the low decay rate of DWD-derived buried wood, we therefore suggest that DWD are contributing to C sequestration (in the form of buried wood) at the rotation scale.

4.4. Management implications

This study highlights the importance of including detrital biomass in our management efforts, and not only focus on live biomass C pools. In Forêt Montmorency, since detrital biomass in early (i.e. 0–20 years) and mid-seral (20–40 years) succession stages contained more C than live biomass, management should pay careful attention to the need to preserve these pools and/or maintain ecosystem processes that contribute to build them.

In addition, forest managers should be aware of the variation of dead wood C stocks through time, and of the moment when total forest ecosystem C stocks are reaching their maximal value (i.e. at age 50 in our experimental conditions at Forêt Montmorency). To promote the climate change mitigation potential of forests, the timing and intensity of harvest should be carefully managed given their high influence on dead wood C legacies and forest C sequestration. Our results showed that rotation length should be at least 50 years and preferably longer, to ensure the build-up of DWD C stocks and that the maximal stand C uptake is reached. Current rotation lengths in the area is typically of 50 years, and sometimes less (around 45 years) with stands being harvested at a premature stage due to operational decisions (e.g. increasing the size of the cutting site to reduce road construction and maintenance costs, thus harvesting both mature and premature stands). Other analyses also suggest that extended rotation lengths may contribute to optimizing the carbon balance of forest management (Assmuth and Tahvonen, 2018; Pingoud et al., 2018). Also, considering the long-term (i.e. 80 years in this study) contribution of DWD to C sequestration, avoiding debris or residue removal should be considered. On the other hand, experimental data on harvest residue removal following clearcuts showed that in Canadian forest conditions, the absolute quantity of debris seem to be mostly driven by stand natural characteristics and processes, rather than by residue removal operations for bioenergy production (Thiffault et al., 2014).

5. Conclusion

This study presented the variation of the relative importance of different carbon pools through time, which also allowed an assessment of the carbon transfers among them in a humid balsam fir boreal forest in southeastern Canada. Despite its inherent and circumstantial limits, the chronosequence approach yielded probative and sensible results. Given the singularity of the Forêt Montmorency in terms of climate (i.e. high precipitation and altitude) and ecological conditions (i.e. scarcity of fires and vigorous, fast decaying moss layer promoting wood burial), our results and management recommendations may not apply to other boreal forests with contrasting conditions (i.e. drier, lower-altitude forests with a high burn rate). The ultimate fate of carbon from downed woody debris and its exact implications in formation of stable soil organic carbon reserves (especially in the fine fraction) are still unclear and deserves further investigation. More empirical research is needed regarding C fluxes between pools, and it is necessary to expand the use of effective tools to assess it, such as compounds tracing methods using C isotopes or other specific markers able to reveal the path of dead wood C from intact to completely decayed states.

Appendix A Ecological and geomorphological characteristics of the chronosequence plots

Plot number	Stand age	Parent material	Granulometry	%Slope	Aspect	Drainage
1	69	Till	Loamy sand	26	274	Good
2	69	Till	Loamy sand	34	270	Good
3	69	Till	Loamy sand	21	270	Good
4	69	Till	Loamy sand	21	280	Good
5	69	Till	Loamy sand	26	256	Good
6	69	Till	Loamy sand	14	292	Good
7	1	Till	Loamy sand	26	274	Good
8	1	Till	Loamy sand	34	270	Good
9	1	Till	Loamy sand	21	270	Good
10	1	Till	Loamy sand	21	280	Good
11	1	Till	Loamy sand	26	256	Good
12	1	Till	Loamy sand	14	292	Good
13	11	Till	Sand	24	261	Medium with seepage
14	5	Till	Sand	30	275	Medium
15	80	Till	Sand	18	324	Medium with seepage
16	73	Till	Sand	24	308	Medium with seepage
17	46	Till	Loamy sand	25	303	Medium
18	43	Till	Loamy sand	20	260	Medium
19	42	Till	Loamy sand	17	308	Medium
20	39	Till	Loamy sand	22	310	Medium
21	36	Till	Loamy sand	24	297	Medium
22	32	Till	Sand	29	240	Medium with seepage
23	31	Till	Sand-Loamy sand	35	238	Medium
24	28	Till	Sand	23	304	Medium
25	26	Till	Loamy sand	16	289	Medium
26	22	Till	Sandy loam	19	288	Medium
27	20	Till	Loam	29	286	Medium
28	18	Till	Loamy sand	21	320	Medium
29	16	Till	Loamy sand	32	300	Medium
30	14	Till	Loamy sand	27	292	Medium
31	68	Till	Loamy sand	23	284	Medium
32	68	Till	Loamy sand	34	252	Medium
33	68	Till	Loamy sand	18	275	Medium
34	68	Till	Loamy sand	32	261	Medium
35	68	Till	Loamy sand	18	291	Medium
36	68	Till	Loamy sand	34	288	Medium

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