

Nine-year changes in carbon dynamics following different intensities of harvesting in boreal aspen stands

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Abstract Mixedwood forests occupy a large extent of boreal regions and have the potential for sequestering large amounts of carbon. In the context of forest ecosystem management, partial cutting prescriptions are increasingly being applied to boreal mixedwood stands. Partial harvesting is expected to maintain carbon pools and dynamics within the limits of those of natural stands. Changes in live tree, deadwood (standing snags, downed logs), forest floor and mineral soil carbon pools were assessed over a 9-year period in a replicated large-scale experiment, which included unharvested controls, two variants of partial harvesting and clear-cuts. We also measured leaf litter and deadwood inputs and decay rates. Carbon flux through leaf litterfall recovered rapidly following partial harvesting. Carbon flux from live trees to deadwood pools was a dominant process in partially harvested stands where snags and downed log carbon pools remained similar to those of natural stands. Hence, the nature of litter inputs diverged strongly among clear-cut and partially harvested treatments. Leaf and wood decay rates were higher in the partial cuts and controls than in clear-cuts. No significant differences in forest floor and mineral soil carbon were observed

9 years after harvesting. Carbon sequestration in live tree biomass was the carbon pool that most strongly differentiated the treatments allowing partial harvesting to maintain forest stands as net carbon sinks.

Introduction

Boreal mixedwoods occupy a large extent of the Canadian boreal region. Because they are found on the warmest and most fertile sites, mixedwood stands are highly productive and are relatively diverse in terms of their tree species composition (Chen and Popadiouk 2002; Bergeron et al. 2014). Hence, they have the potential to sequester large amounts of carbon (C) (Cavard et al. 2010; Laganière et al. 2013). In response to a range of environmental concerns that are related to the widespread application of even-aged forest management, forest ecosystem management approaches (FEM) have been proposed for the Canadian boreal mixedwoods (Bergeron and Harvey 1997; Perera et al. 2004; Work et al. 2004). Forest ecosystem management relies upon the diversification of silvicultural systems at the landscape level, including various forms of partial cutting (Lieffers and Beck Jr 1994; Bergeron and Harvey 1997). At the stand level, it is assumed that harvesting prescriptions retaining forest structure that is similar to pre-harvest conditions allow the maintenance of ecosystem functions within their range of historical variability (Drever et al. 2006; Gauthier et al. 2008). On the other hand, it is believed that managing forests for C sequestration has the potential to reduce atmospheric CO₂ concentrations (Schwenk et al. 2012). In this context, the implications of FEM for C dynamics, and more particularly the effects of partial harvesting, need to be investigated (Lee et al. 2002).

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Harvesting has immediate and direct effects on ecosystem C pools, including a decrease in above-ground biomass (Zhou et al. 2013) and an increase in the quantity of logging slash (Brais et al. 2004) and dead roots (DesRochers and Lieffers 2001b). In partial cuts, changes in the characteristics of residual live stems (Bose et al. 2014b) can result in decreased net primary productivity (Balboa-Murias et al. 2006) and increased mortality (Bose et al. 2014b), which may negatively affect the tree C pool. Depending upon its intensity, harvesting also alters temperature and moisture regimes (Prévost and Pothier 2003; Brais et al. 2004) and forest floor biological activity (Sitonen 2001; Sippola et al. 2004), which in turn affect organic matter (OM) decomposition rates (Prescott 1997). However, a consensus on how stand conditions following harvesting affect decomposition rates has yet to emerge, given that studies have produced equivocal outcomes (Wei et al. 1997; Hope et al. 2003; Shorohova et al. 2008). A significant factor that influences decomposition is OM quality, which is often characterised by its C:N ratio. The ratio differs by an order of magnitude between fresh leaf litter and logs (Strukelj et al. 2012). Because partial harvesting exerts fewer effects on leaf litterfall, on deadwood production and on microclimate (Lee et al. 2002; Brais et al. 2004) than does clear-cutting, its effect on the rate of OM decomposition might also be limited (Hope et al. 2003).

Assessing long-term effects of harvesting on soil C storage can be problematic, given the large spatial variation in soil C pools (Diochon et al. 2009). Increased litter decomposition, decreased litter inputs and mixing of the forest floor with mineral soil can cause a decline in forest floor C pools (Yanai et al. 2003). Recent meta-analysis has revealed a consistent reduction of ~30 % in forest floor C pools following clear-cut harvesting of temperate forests, whereas less consistent changes occurred in the mineral soil (Nave et al. 2010). In contrast, decreases in soil C storage were found to be of low magnitude following partial harvesting (Zhou et al. 2013). Yet, most studies reporting changes in soil C pools that follow harvesting lack comprehensive information on C fluxes (Nave et al. 2010; Zhou et al. 2013). Also, few studies so far have targeted boreal mixedwoods (Lee et al. 2002).

Integration of concomitant changes in stand growth, deadwood and leaf litter inputs, and organic matter decomposition would improve our understanding of ecosystem C pools and mechanisms of soil C sequestration following harvesting (Seedre et al. 2011). The SAFE (Sylviculture et aménagement forestier écosystémique) project (Brais et al. 2004, 2013) is a series of experiments conducted in the eastern Canadian boreal mixedwood forest that aim to test a FEM approach developed for the region (Bergeron and Harvey 1997). In 1998, the first phase

of SAFE was established in even-aged stands of trembling aspen (*Populus tremuloides* Michx.). Treatments include four intensities of harvesting, and C pools and fluxes in the experimental units have been monitored since 1998. We attempted to answer the following questions: What are the effects of clear-cut and partial harvesting in the medium term (over the 9-year period) (1) on stand C fluxes; (2) on stand C pools; and (3) on stand C balance?

We hypothesised the following: (1) A decrease in leaf litterfall and an increase in fine woody debris immediately after harvesting would follow a gradient of harvesting intensity. (2) We also anticipated that snag and downed log characteristics and recruitment in partially harvested stands would be reduced but close to those of undisturbed control (Rouvinen et al. 2002). (3) Due to the capacity of aspen stands to re-establish their leaf biomass through suckering following disturbance, we expected leaf litterfall to reach similar levels rapidly in all treatments (Covington and Aber 1980). Therefore, the importance of leaf litterfall relative to that of deadwood recruitment would increase with an increasing level of harvesting. This would decrease the C:N ratios of the forest floor and mineral soil organic matter, in turn (Strukelj et al. 2012). (4) With an increasing level of harvesting, we also projected an increase in the decay rates of logs and leaf litter (Hope et al. 2003; Yanai et al. 2003). (5) Partially harvested stands would maintain overall live tree, deadwood and soil C pools closer to those of control than clear-cuts. (6) The intensity of harvesting would control stand C balance between C inputs through net primary productivity and C outputs through decomposition and will determine whether stands act as C sinks or sources.

Materials and methods

Study area

The study was located in the Lake Duparquet Research and Teaching Forest (LDRTF; 48°86'N–48°32'N, 79°19'W–79°30'W). LDRTF lies within the Abitibi region of north-western Quebec. Regional climate is continental with a mean annual temperature of 0.7 °C. Mean temperature of the warmest and coldest months is 16.9 °C (July) and –18.2 °C (January), respectively. Annual precipitation is 890 mm, of which 614 mm falls as rain from April to November (Environment Canada 2010). The region is situated in the mixedwood zone of the Boreal Shield, within the balsam fir-white birch bioclimatic domain. The study soils are formed in deep fine clayey to fine loamy textured glacio-lacustrine deposits that formed through sedimentation at the bottom of glacial Lake Barlow-Ojibway (Veillette et al. 2000) under fresh to moist moisture regimes

(Brais and Camiré 1992). Soils are classified as Grey Luvisols (Soil Classification Working Group 1998; Boralfs, USDA classification system). They are characterised by an Ahe horizon (0–5 cm depth) and a Bt horizon (5–20 cm depth) (Bergeron et al. 1983). The soil matrix is free of coarse fragments (>2 mm). Forest floor thickness ranges from 5 to 10 cm, and the surface mineral soil pH ranges from 4.5 to 4.75 (Brais et al. 2004 should be consulted for greater details of the soil characteristics).

Experimental design and treatments

This study was conducted in aspen-dominated stands of fire origin that dated from 1923 (Table 1; for a complete description of the harvested stands, see Brais et al. 2004). Four levels of forest harvesting were applied in the winter of 1998–1999, according to a complete block design with three replications per treatment, with experimental units ranging from 1 to 2.5 ha in area. Treatments included a control (Control), a clear-cut (CC) and two partial cut treatments. Pre-harvest basal areas were lower in the partial cuts than in the two other treatments (Table 1). Harvesting of stems (>9 cm dbh) removed, respectively, 31 % (1/3 PC) and 62 % (2/3 PC) of basal area, compared to controls. Non-vigorous aspen stems were preferentially removed in the 1/3 PC treatment, while stands in the 2/3 PC treatment were crown-thinned with larger, vigorous aspen stems being preferentially selected (Table 1). In all harvesting treatments, stems were delimited on site.

Field methods

Live stem and snag inventories

In autumn 1998 (before harvesting), five permanent circular sampling plots (PSP, 400 m², radius = 11.28 m) were established in each experimental unit, for a total of 60 PSP. Within each PSP, all live trees ≥5.0 cm dbh (diameter at breast height, 1.3 m) were identified to species, measured (dbh) and tagged for further measurements. In the north-east quadrant of each plot (100 m²), all stems with dbh ranging from 2.0 to 4.99 cm were identified to species, measured (dbh) and tagged. In spring 1999 (after harvesting), a tally of stems remaining in all PSP was conducted in the partial cuts to estimate residual basal area and changes in stem density. Forest inventories were conducted again in the autumn of 2001, 2004 and 2007.

From 2001 to 2007, a similar inventory was conducted for snags within PSP. Snags (dead stems >1.3 m in height) were identified to species, measured (dbh) and tagged. In 2007, snags were also measured for height and assigned to one of five decay classes, from class S-I that represented fresh snags to class S-V for well-decomposed snags (Strukelj et al. 2013). All stems that bore no tags in 2001 were assumed to have been dead and standing at the time of the tally (1999). Pre-harvest (1998) values for snags in partial and clear-cut experimental units could not be reconstructed, and consequently, the average value that had been determined for the control experimental units in 1999 was attributed to all treatments for 1998.

Table 1 Characteristics of boreal aspen stands before and immediately after partial cut (PC) and clear-cut (CC) harvesting, together with carbon fluxes associated with harvesting

	Control	1/3 PC	2/3 PC	CC
Pre-harvest stand basal area (m ² ha ⁻¹)	44.95 (1.79)	41.31 (3.27)	38.52 (2.26)	43.43 (6.08)
Residual standing stems (dbh ≥ 2 cm)				
Basal area of trees ≤20 cm (m ² ha ⁻¹)	8.87 (2.08)	6.55 (2.63)	8.11 (2.39)	0.03 (0.03)
Basal area of trees >20 cm (m ² ha ⁻¹)	36.08 (2.13)	24.64 (4.48)	8.94 (3.89)	0
Total tree basal area (m ² ha ⁻¹)	44.95 (1.79)	31.19 (1.92)	17.05 (1.59)	0.03 (0.03)
Total snag basal area (m ² ha ⁻¹)	2.80 (0.96)	2.46 (0.83)	3.30 (1.90)	0.10 (0.09)
Downed logs (diameter ≥ 0.5 cm)				
Volume of logs < 2.5 cm (m ³ ha ⁻¹)	7.79 (0.77)	9.28 (1.32)	13.90 (4.58)	31.06 (9.55)
Volume of logs ≥ 2.5 cm (m ³ ha ⁻¹)	96.04 (63.56)	122.92 (30.55)	93.02 (8.25)	155.65 (44.62)
Harvested stems (dbh ≥ 9 cm)				
Basal area of harvested stems (m ² ha ⁻¹)	0	10.12 (1.35)	21.47 (0.67)	43.40 (6.05)
Mass of exported stems (MgC ha ⁻¹)	0	20.03 (2.45)	45.33 (3.39)	86.61 (11.54)
Mass of logging slash (MgC ha ⁻¹)	0	2.52 (0.33)	5.66 (0.64)	11.34 (1.41)
Mass of root input (MgC ha ⁻¹)	0	6.15 (0.75)	13.66 (0.18)	26.27 (3.50)

Mean values and standard deviations (in parentheses)

Downed log inventory

Inventories of downed logs were conducted in 1998 (before harvesting), in 1999 (after harvesting), and again in 2001, 2004 and 2007. The volume of downed logs was estimated by the triangular transect method (Van Wagner 1982). One triangle (30 m a side) was sampled in each experimental unit (total length of 90 m), except in 2007 when two triangles were sampled in each experimental unit (180 m length). Along each transect, the frequency of downed logs was recorded by species, diameter class and decay class. Mid-points of the diameter classes were 5 cm (2.5–7.5 cm), 10 cm (7.6–12.5 cm), 15 cm (12.6–17.5 cm) and 20 cm (>17.6 cm). In 1999, an additional diameter class (1.5 cm, 0.5–2.4 cm) was recorded. Decay classes were characterised by a five-class system based on visual criteria (Strukelj et al. 2013), from class L-I for fresh logs to class L-V for well-decomposed logs.

Soil sampling

In 1998 (before harvesting), 1999 (first year after harvesting) and 2007, soils were sampled for the determination of dry mass, and N and C content. The forest floor and uppermost 10 cm of mineral soil were sampled 12 m from the PSP centre in two opposite directions, for a total of 120 samples per sampling date and per soil horizon. Prior to sampling, all live plant material and the L-layer (fresh leaves and woody debris) were removed. Forest floor, including all organic material (FH layers) lying on top of the mineral soil, was manually extracted within 25 × 25 cm micro-quadrats and weighed in the field. In 2007, we proceeded in a similar manner with the alignic forest floor (i.e. originating from fine litter) while the lignic forest floor (i.e. originating from woody debris) was sampled separately within a 71 × 71 cm micro-quadrat, to take into account its greater heterogeneity. Lignic forest floor was recognisable by its distinct red to brown colour and fibrous texture. At each sampling location ($n = 120$), a bulk sample of forest floor (individual alignic and lignic samples in 2007) and a bulk sample of mineral soil (0–10 cm) were taken for dry mass estimation and laboratory analyses. In 1998, an additional undisturbed soil sample (5 cm diameter, 100 cm³) was also taken at each sampling location between 0 and 10 cm depth in the mineral soil with a stainless-steel double-cylinder soil sampler (Eijkelpamp Agrisearch Equipment, Giesbeek, The Netherlands) for bulk density determination. Upon collection, samples were immediately brought to the laboratory where they were air-dried for analyses.

Leaf litterfall

In the summer of 1999, one litter trap (0.5 m²) was positioned in the centre of each PSP for a total of 60 litter traps.

Litter traps were made of fibreglass screen (1-mm aperture mesh) that allowed rapid drainage of rainfall. Litter was collected twice a year from spring 1999 to spring 2002 and from spring 2005 to spring 2008. Leaf litter was collected immediately after litter fall, which generally occurs in October over a 2-week period in these aspen stands, and a second time in May following spring snow melt.

Leaf and wood decomposition rates

Freshly fallen leaves of aspen were collected in autumn 1999, whereas wood blocks were cut (10 × 5 × 5 cm) from dimensional aspen lumber. Leaf litter (± 10 g) and wood blocks (100–150 g) were enclosed in litterbags ($\pm 10 \times 8$ cm) made of fibreglass (1-mm aperture mesh), with their initial moist mass imprinted on plastic tape (DYMO Inc.). Five subsamples of each litter type were dried (48 h, 65 °C) to determine the moist-to-dry mass conversion factors and to characterise initial litter chemical composition. In autumn 1999, five litterbags containing wood blocks and five containing leaves were placed on the litter layer in each PSP and were left to decompose in situ. A total of 240 litterbags were retrieved 1, 3, 5 and 6 years after the start of the experiment.

Laboratory methods

Leaves that were collected from the litter traps were dried (48 h, 65 °C) and weighed. After litterbag collection, the exterior was carefully cleaned with a brush. Decayed leaf litter or wood blocks were removed from the bags, manually sorted to eliminate any mineral soil or plant remains, dried (48 h, 65 °C) and weighed. Initial moist weights of leaf litter and wood blocks were corrected for their respective moisture contents. For each collection date, materials from litter traps and from leaf and wood litterbags were pooled over experimental units. Samples were ground to pass a 0.5-mm mesh for C analyses.

Undisturbed 100 cm³ soil samples were dried (48 h, 105 °C) and weighed to determine bulk density. No correction was necessary for coarse fragments. Subsamples of the forest floor were weighed before and after drying (48 h, 65 °C) to determine gravimetric moisture content. Forest floor masses that were measured in the field were corrected for moisture content.

The remaining samples of forest floor and mineral soil (0–10 cm) were air-dried (20–25 °C), sieved to 2 mm before grinding to 250 μ m and analysed. In 1998 and 1999, soil C and N concentrations were determined following wet-digestion (Parkinson and Allen 1975). In 2007, C and N analyses were conducted by high-temperature dry combustion using an elemental analyser (LECO, St. Joseph, MI).

Calculations

Carbon pools

Above-ground biomass of live trees and snags was estimated using specific allometric equations that were based on dbh (Lambert et al. 2005), whereas the mass of coarse roots was estimated using allometric equations of Brassard et al. (2011) and Bond-Lamberty et al. (2002). Above-ground mass of each tree was assessed by adding the mass of stems (wood and bark) and branches. Leaves were not included in the tree C pools. Snag mass was assessed with the same equations, but excluded some tree components as implied by our snag classification criteria (Strukelj et al. 2013). Mass of snags in decay classes S-I and S-II included stems and branches, but 50 % of branch mass was removed for snags of decay class S-II. Mass of snags in decay classes S-III, S-IV and S-V was estimated with the stem equations, but 33, 66 and 100 % of bark mass were removed, respectively. Percentage loss of wood density that corresponded to a snag decay class (Angers et al. 2012a) was applied to the estimated snag mass, using the wood density of decay class S-I as an initial value. The mass of snags in decay classes S-III, S-IV and S-V with broken tops was further reduced by a factor corresponding to the ratio of their remaining volume to that of an intact pole of the same dbh. The volume of snags was estimated as the frustum of a paraboloid (Husch et al. 2003), using the estimated initial height (Poulin et al. 2008; Beaudet et al. 2011) and the measured height of the snag. Mass loss during decomposition of dead roots was estimated using decay rates that were taken from the study of Shorohova et al. (2008).

The C pool of live trees was estimated from their biomass and from specific C concentrations that were obtained by Lamtom and Savidge (2003). For species that were not reported, we used C concentrations of species within the same genera. The same C concentrations were used for snags, given that a previous study found no changes in C concentrations with snag decay (Strukelj et al. 2013). To estimate the above-ground C pool of snags in 1999, 2001 and 2004, where the height and decay class of snags were not determined, we estimated the C content of snags in each PSP from their basal areas, using a regression between basal area and C content that had been obtained from data collected in 2007 ($R^2 = 88\%$).

Density of downed logs was based on values that were determined from parallel studies (Brais et al. 2004; Harvey and Brais 2007) that were conducted for each combination of species and decomposition class. Changes in C concentrations of logs with decomposition were assessed in a previous study (Strukelj et al. 2013).

The C pool of the forest floor was calculated by multiplying the C concentration by the dry mass of material. The C pool of the mineral soil (0–10 cm) was estimated by multiplying its C concentration by its bulk density and by the volume of the 0–10 cm mineral soil. As pre-harvest values of bulk density were used in all calculations, changes in mineral soil (0–10 cm) C pools would result from changes in C concentrations only.

Carbon fluxes

Carbon fluxes that were incurred by harvesting were estimated using specific allometric equations, which were based on harvested tree dbh (Bond-Lamberty et al. 2002; Lambert et al. 2005; Brassard et al. 2011). Carbon flux from live trees to logging slash and to dead roots included the C masses of branches and tree roots from the harvested trees, respectively, whereas C flux from live trees to forest products included C masses of stem wood and stem bark. Carbon fluxes from live trees to deadwood that were incurred through tree mortality were based on the same equations (branches, stem wood and stem bark; Lambert et al. 2005) and from changes in tree status between forest inventories over the 9-year period.

Carbon content of annual leaf litterfall was obtained by multiplying measured C concentrations by the dry mass of the litterfall. To obtain cumulative C fluxes that were associated with leaf litterfall over the 9 years following treatment, leaf litterfall from 2002 to 2005 was estimated by considering (for each PSP) a linear increase or decrease in leaf litterfall between data that had been obtained for 2002 and for 2005.

The C content of each decomposition litterbag was estimated from its mass and C concentration at the time of sampling. Residual C (%) in litterbags is the ratio of C content at the time of sampling divided by the initial C content.

Data analyses

The effects of harvesting on the response variables were assessed by means of linear mixed-effects models and Wald t tests ($\alpha = 0.05$; Pinheiro and Bates 2000) using the lme function that is included in the nlme library of R (R Development Core Team 2012). Fixed factors in the models included treatment (control, 1/3 partial cut, 2/3 partial cut, clear-cut), time-since-treatment and their interaction. Leaf litterfall was analysed as a function of residual tree basal area, basal area-squared, time-since-harvesting, and the interactions between basal area and time. Carbon pools in forest floor and mineral soil were analysed separately in 1999 and 2007, due to differences in the methods of C and N analysis, and, consequently, no

inferences for a time effect could be made. Carbon remaining from decomposition was analysed as a function of time in the field, treatment, material (wood vs leaves) and their interactions, using a negative exponential model (i.e. log-transformation of the response variable). Interactions were removed from all models when their p values were >0.10 . For C pools, pre-harvest values (1998) of the response variables were used as covariates to account for pre-harvest differences among experimental units, but were removed when they were not significant. When treatment was used as a categorical fixed factor, the reference level of treatment was control, against which the three other treatments were compared.

Random factors included sampling plots, which were nested within experimental unit, and experimental units, which were nested within block, except for logs that were sampled at the experimental unit scale. Normality and homogeneity of variance assumptions were verified by visual assessment of residuals. When these assumptions were not met, logarithmic or square root transformation was applied.

In the clear-cut experimental units, C pools of snags and large trees, together with C fluxes incurred through tree mortality, were negligible. Therefore, the clear-cut treatment was removed from the statistical analyses to respect the homoscedasticity assumption. Nevertheless, observed values are presented in Figs. 1 and 3 for the sake of comparison.

Results

Carbon fluxes directly caused by logging

Tree harvesting exported 20.0, 45.3 and 86.6 MgC ha⁻¹ in forest products from the 1/3 PC, 2/3 PC and CC treatments, respectively (Table 1). Fresh logs were absent prior to harvesting, but on-site de-limbing of stems left fresh branches and tree tops on the ground, which corresponded to C inputs of 2.5, 5.7 and 11.3 MgC ha⁻¹ in the 1/3 PC, 2/3 PC and CC treatments, respectively (Table 1). Harvesting also caused an influx of dead roots into the soil (Table 1).

Carbon fluxes through tree mortality and leaf litterfall after harvesting

During the first year following harvesting (1999), annual C fluxes through leaf litterfall decreased with decreasing residual basal area ($p < 0.001$, Table 2a). The fluxes averaged 1.34, 1.10, 0.72 and 0.07 MgC ha⁻¹ year⁻¹ in the control, 1/3 PC, 2/3 PC and CC treatments, respectively (Fig. 1a). Leaf litterfall increased ($p < 0.001$) with basal

area. However, 9 years after harvesting, the increase was less pronounced in stands that had a large basal area and even decreased in stands with basal areas greater than 35 m² ha⁻¹ ($p < 0.001$, Table 2a). Nine years after harvest, annual C fluxes through the leaf litterfall averaged 1.27, 1.27, 1.04 and 0.65 MgC ha⁻¹ year⁻¹ in the control, 1/3 PC, 2/3 PC and CC treatments, respectively (Fig. 1a). Few differences were observed between partial cuts and controls in terms of leaf litterfall, although basal areas remained very different among treatments.

During the first 3 years following harvesting, C fluxes that were associated with tree mortality were higher in the 2/3 PC treatment than in the control, but decreased thereafter (Table 2b; Fig. 1b). In the control and 1/3 PC treatments, tree mortality increased with time-since-harvesting, particularly in the control, but decreased after the 6 year following harvesting (Table 2b). From years 6 to 9, tree mortality reflected the remaining basal area ($p < 0.001$) in the control and partial cut treatments (Fig. 1b).

Over the 9 years that followed harvesting, cumulative C inputs to leaf litter increased almost fivefold with increasing basal area, from 2.7 MgC ha⁻¹ in the clear-cut to 12.2 MgC ha⁻¹ in the control, whereas C inputs to dead roots decreased with increasing basal area (Table 2c; Fig. 1c). Total C fluxes from tree biomass to the deadwood pool through logging slash and tree mortality were higher in the 2/3 PC than in the control ($p = 0.014$), while other treatments were similar to the control (Table 2c; Fig. 1c). Following clear-cutting, C fluxes to the deadwood pool were associated with logging slash and mortality of shrubs and small trees during harvesting operations and remained close to 0 thereafter (Fig. 1b, c).

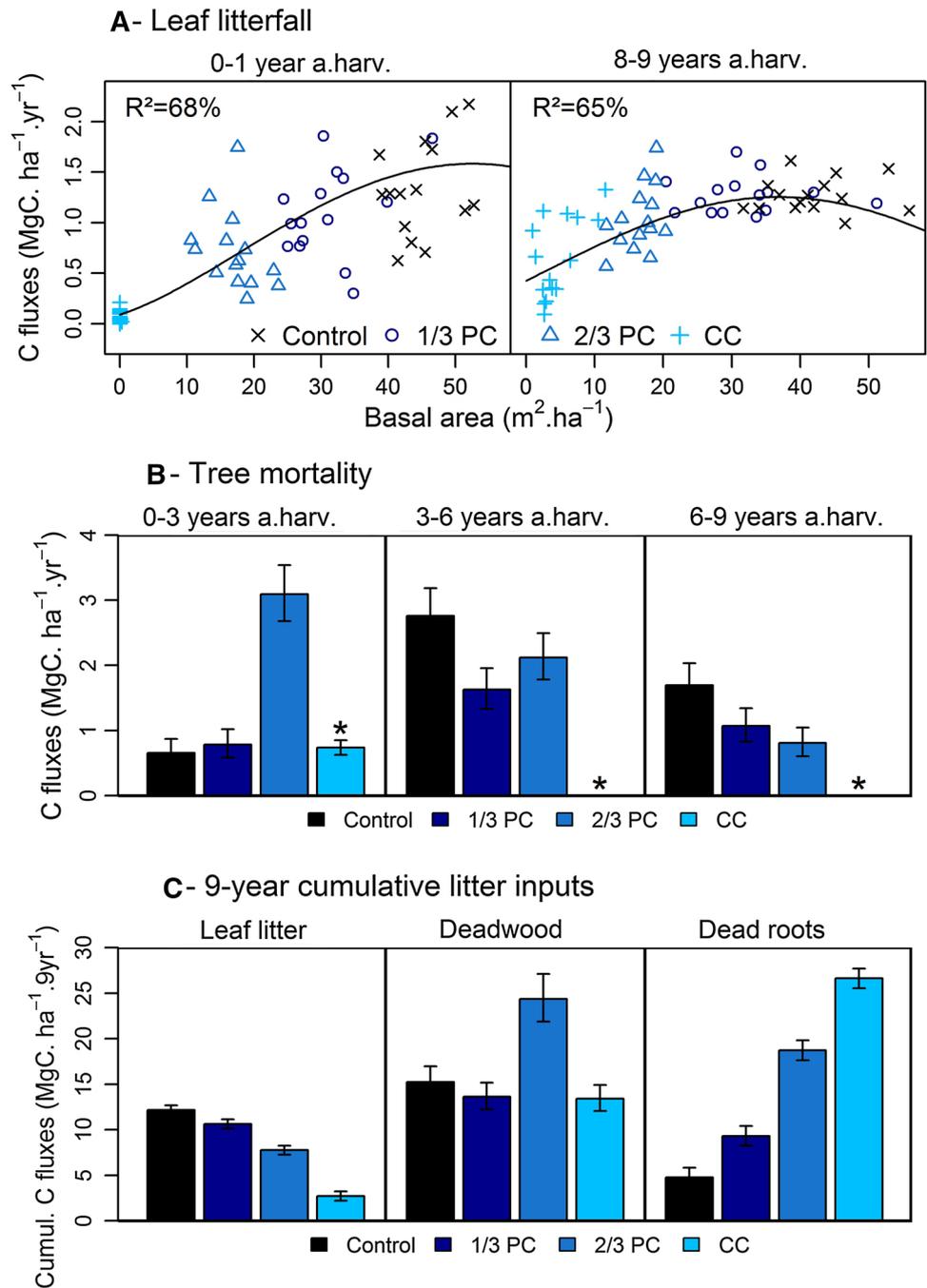
Carbon fluxes through decomposition after harvesting

Estimates of the decay rates of aspen leaves and wood were similar (Table 2d; Fig. 2). Only clear-cuts had decomposition rates (0.13 year⁻¹) that differed from the controls (0.19 year⁻¹). After 6 years of decomposition, total C mineralised from decaying leaves and wood averaged 75 % of initial C content in the control, 1/3 PC and 2/3 PC treatments, and 65 % in the CC. Initial C contents that were predicted by the negative exponential models were lower than 100 % in all treatments.

Changes in carbon pools of tree biomass after harvesting

The C pool of small trees (2 cm < dbh ≤ 20 cm) was initially reduced in the clear-cuts compared to the control, but increased significantly with time, from 0 immediately after harvesting to 3.8 MgC ha⁻¹ 9 years later (Table 3; Fig. 3a).

Fig. 1 Effects of partial cut (PC) and clear-cut (CC) harvesting on ecosystem C fluxes over a 9-year period following harvesting in boreal aspen stands. **a** Carbon fluxes associated with annual leaf litterfall during the first and the ninth years following harvesting. **b** Carbon fluxes associated with annual tree mortality between 0 and 3, 3 and 6, and 6 and 9 years after harvesting. **c** Nine-year cumulative C fluxes from tree biomass to leaf litter (leaf litterfall), to deadwood (logging debris and tree mortality) and to dead roots (logging debris and tree mortality). *Note:* * Clear-cut values are observed values, as they were removed from the statistical analyses (close to 0). *a.harv.* after harvesting



In the 2/3 PC, the small tree C pool first decreased and then increased from year 6 onwards. Small tree C pools decreased in the 1/3 PC and control over the 9-year period (Table 3).

The C pool that was associated with large trees (dbh > 20 cm) was reduced by all harvesting treatments (Tables 1, 3; Fig. 3b). Over the following 9 years, the C pool of large trees remained more or less constant in partially harvested and control stands ($p = 0.109$, Table 3) and remained close to 0 in the clear-cuts.

Over the 9-year period, the total tree biomass C pool (stem > 2 cm dbh) did not change significantly in the controls and 1/3 PC (Table 3; Fig. 3c). In the 2/3 PC, the live tree C pool first decreased before increasing from year 6 after harvesting and onward. The C pool in tree biomass after clear-cutting followed the pattern of the small tree C pools. Trees >20 cm (dbh) accounted for most of the tree biomass C over the 9-year period in the controls and partial cuts. Nine years following harvest, total tree biomass C pools were

Table 2 Effects of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on annual and cumulative C fluxes associated with leaf litterfall, tree mortality, snag fall and decomposition, which were assessed with linear mixed models

<i>(a) Annual leaf litterfall as a function of residual stand basal area (BA), BA², time-since-harvesting and their interaction</i>											
Variable	BA		BA ²		Time		BA × Time				
Leaf litterfall ^a	0.0371***		−0.0003***		0.0440***		−0.0014***				
<i>(b) Annual tree mortality as a function of treatment, time-since-harvesting, time-squared and their interactions with treatment</i>											
Variable	1/3 PC	2/3 PC	Time	Time ²	Interaction: Time ×		Interaction: Time ² ×				
					1/3 PC	2/3 PC	1/3 PC	2/3 PC			
Tree mortality ^a	0.599 ^{NS}	2.074**	0.802***	−0.084***	−0.409 ⁺	−0.858***	0.041 ^{NS}	0.072**			
<i>(c) Cumulative C fluxes associated with leaf litterfall, tree mortality, and snag fall over nine years following harvesting as a function of treatment</i>											
Variable	1/3 PC		2/3 PC		CC						
C flux through leaf litterfall	−1.527 ⁺		−4.404***		−9.461***						
C flux from live trees to snags ^{a, b}	−0.720 ^{NS}		0.193 ^{NS}								
C flux from live trees to downed logs ^a	0.042 ^{NS}		0.398 ⁺		0.195 ^{NS}						
C flux from snags to downed logs ^{a, b}	−0.213 ^{NS}		0.172 ^{NS}								
Total C flux from live trees to deadwood ^{c, d}	−0.111 ^{NS}		0.469*		−0.128 ^{NS}						
Total C flux from live roots to dead roots ^d	4.567**		13.975***		21.880***						
<i>(d) C remaining from decaying material as a function of treatment, material (leaf vs wood), time of decay, and their interactions with treatment</i>											
Variable	1/3PC	2/3PC	CC	Time	Material	Interaction: Time ×			Interaction: Material ×		
						1/3PC	2/3PC	CC	1/3PC	2/3PC	CC
C remaining ^c	−0.07 ^{NS}	0.08 ^{NS}	0.02 ^{NS}	−0.19***	0.10 ^{NS}	0.004 ^{NS}	−0.0001 ^{NS}	0.07*	0.03 ^{NS}	−0.20 ^{NS}	−0.25 ⁺

The parameter estimates of the model are indicated with their *p* values. ****p* < 0.001; ** 0.001 < *p* < 0.010; * 0.010 < *p* < 0.050; ⁺ 0.050 < *p* < 0.100; ^{NS} *p* > 0.100. The reference level was control for treatment and leaf litter for material

^a Square-root transformation

^b Clear-cutting treatment excluded from the model, because values = 0

^c Logarithmic transformation

^d Including C fluxes that were associated with tree mortality and logging debris

96.1, 76.8, 36.3 and 3.9 MgC ha^{−1} in control stands and in stands following 1/3 PC, 2/3 PC and CC, respectively.

Changes in carbon pools of snags and downed logs after harvesting

Carbon pools of small and large snags increased in both partial harvesting treatments and in the control over the 9 years post-harvest, but the increase was not significant for large snags (Table 3; Fig. 3d, e). The C pool of snags remained negligible over the 9 years following CC. The C pool of large snags in the control was similar to both partial cutting treatments (Table 3). Nine years after harvest, few differences in small snags remained among treatments (Fig. 3d), whereas the C pool of large snags was smaller in the 2/3 PC than in the control.

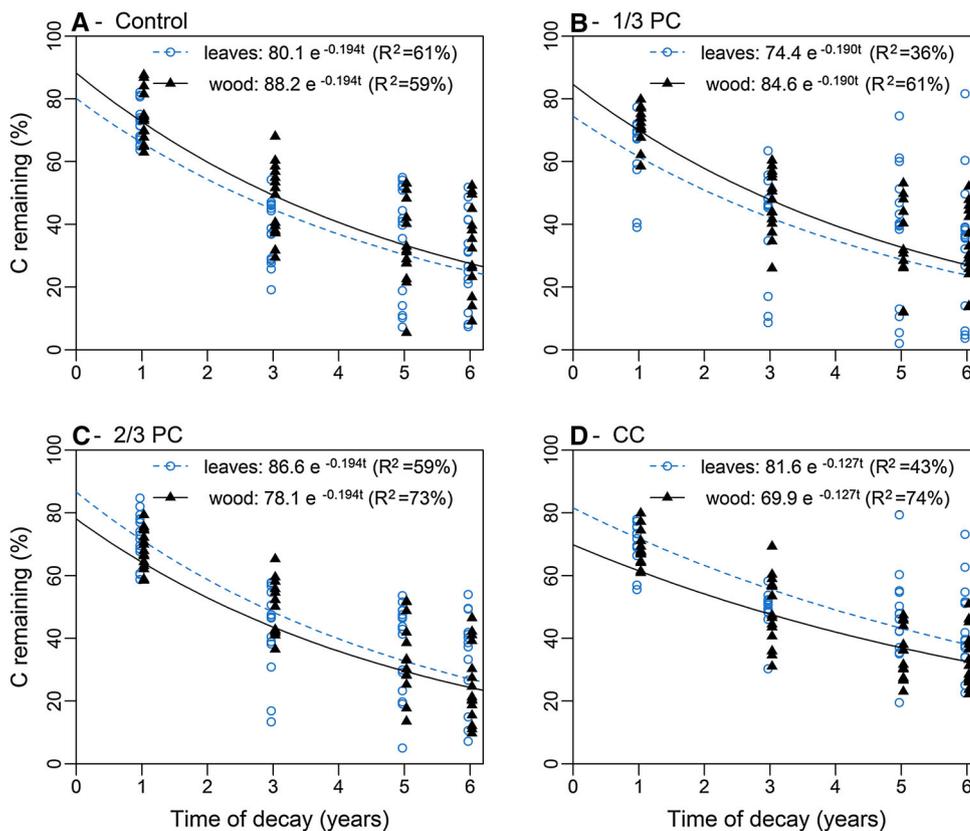
Carbon fluxes from snags to downed logs averaged 0.96, 0.58 and 1.33 MgC ha^{−1} over the 9-year period in the

control, 1/3 PC and 2/3 PC treatments, respectively. However, differences between control and partial harvesting treatments were not significant (Table 2).

The C pool of small logs was initially larger in clear-cuts than in controls (Table 3) and significantly decreased with time-since-harvesting. After 9 years, the C pool of small logs attained similar values in all treatments (Table 3; Fig. 3g). The C pool of large downed logs was initially larger in the 1/3 PC than in the control (*p* = 0.042), but did not differ between the control and other treatments (Table 3; Fig. 3h). With time-since-harvesting, the C pool of large downed logs increased significantly in the control (*p* = 0.014), while decreasing in the partial cuts and clear-cut (Table 3).

The C pool of fresh downed logs decreased with time-since-treatment (*p* < 0.001), more strongly so in the treatments that had higher inputs during harvesting (Table 3). After 9 years, few differences remained among

Fig. 2 Effects of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on C mineralisation from decaying aspen leaf litter and wood. *Note:* Values of C remaining are expressed as the proportion (%) of initial decomposition bag C content



treatments. The C pool of moderately decayed logs increased in all treatments with time-since-harvesting ($p = 0.030$), more strongly in the 2/3 PC and control treatments, while the increase slowed down and decreased in the two other treatments (Table 3). The C pool of well-decayed logs increased following partial cut and control treatments and reached a plateau after 6 years (Table 3).

During the 9 years following harvesting, the C pool of downed logs decreased in the clear-cuts, but did not change significantly in the other treatments (Table 3; Fig. 2i). Moreover, the ratio of snags to logs did not differ among treatments (not shown), nor did the C fluxes differ from live trees to snags (Table 2). Over 9 years, C fluxes from live trees to downed logs averaged 1.47, 1.58, 2.57 and 1.15 MgC ha⁻¹ in the control, 1/3 PC, 2/3 PC and CC treatments, respectively.

Changes in carbon pools of forest floor and 0–10 cm mineral soil after harvesting

The increase in forest floor C pool that was observed the first year following harvesting was significant in clear-cut stands, but not in partial harvesting treatments (Table 4; Fig. 4a). In 2007, differences in the C pool of the forest floor between harvesting treatments and control were of the same order of magnitude as was observed in 1999, but with

greater variability, which resulted in no significant treatment effect (Fig. 4a). Also, C pools in alignic and lignic forest floors did not differ between the control and harvesting treatments (Table 4). The C:N ratio of the forest floor did not differ between the control and harvesting treatments in 1999, as well as in 2007 (Table 4).

Carbon pools in the mineral soil did not differ among control and harvesting treatments in 1999 and 2007 (Table 4; Fig. 4b). The mineral soil C:N ratio did not differ among treatments in 1999 and in 2007 (Table 4).

Net changes in total C pools after harvesting

The balance between losses and gains of C between pre- and post-harvest conditions showed net ecosystem losses of C with harvesting while control C pools remained stable (Fig. 5a). Over the 9 years following harvesting, increases in snag C pools were observed in the control and partial cut treatments, whereas decreases in log C pools were found in the 1/3 PC and the CC treatments (Fig. 5b). Tree biomass accumulated in the 1/3 PC and CC treatments, but decreased in the control and 2/3 PC treatment. There were net ecosystem losses of C in the 2/3 PC and the CC treatments, and net gains in the two other treatments (Fig. 5b). After 9 years, dead OM C pools were very similar between the control and harvesting treatments, whereas large

Table 3 Effect of partial cut (PC) and clear-cut (CC) harvesting on boreal aspen stands and time-since-harvesting on aboveground standing C pools, assessed by means of linear mixed models

Variable	Pre-harvest			Time			Time ²			Interaction: Time ×			Interaction: Time ² ×		
	1/3PC	2/3PC	CC	CC	2/3PC	CC	CC	2/3PC	CC	1/3PC	2/3PC	CC	1/3PC	2/3PC	CC
Trees															
Small ^a	0.051***	-0.746*	-0.358 ^{NS}	-4.136***	-0.185**	0.004 ^{NS}	0.004 ^{NS}	0.026 ^{NS}	-0.232**	0.129 ^{NS}	0.00004 ^{NS}	0.027***	0.00004 ^{NS}	0.027***	0.029***
Large ^{a, b}	0.052***	-1.109**	-4.072***	0.021 ^{NS}	0.043 ⁺	0.044 ^{NS}	0.043 ⁺	0.043 ⁺	0.044 ^{NS}	0.044 ^{NS}	0.043 ⁺	0.044 ^{NS}	0.043 ⁺	0.044 ^{NS}	0.044 ^{NS}
Total ^a	0.038***	-1.454**	-3.703***	-9.999***	-0.003 ^{NS}	-0.003 ^{NS}	-0.003 ^{NS}	0.053 ^{NS}	-0.157*	-0.055 ^{NS}	-0.0005 ^{NS}	0.017*	-0.0005 ^{NS}	0.017*	0.036***
Snags															
Small ^{a, b}	-0.004 ^{NS}	0.120 ^{NS}	0.169**	0.169**	0.010 ⁺	0.050 ^{NS}	-0.163*	0.050 ^{NS}	0.050 ^{NS}	0.050 ^{NS}	0.018*	-0.010 ^{NS}	0.018*	-0.010 ^{NS}	-0.010 ^{NS}
Large ^{a, b}	-0.025 ^{NS}	0.225 ^{NS}	0.066 ^{NS}	0.066 ^{NS}	0.009 ^{NS}	0.009 ^{NS}	0.066 ^{NS}	0.009 ^{NS}	0.066 ^{NS}	0.009 ^{NS}	-0.003 ^{NS}	-0.011*	-0.003 ^{NS}	-0.011*	-0.011*
Total ^{a, b}	-0.240 ^{NS}	0.261 ^{NS}	0.144**	0.144**	0.002 ^{NS}	0.002 ^{NS}	0.144**	0.002 ^{NS}	0.144**	0.002 ^{NS}	-0.001 ^{NS}	-0.012**	-0.001 ^{NS}	-0.012**	-0.012**
Logs															
Small	4.364 ^{NS}	3.288 ^{NS}	17.467***	17.467***	-1.031 ^{NS}	0.115 ^{NS}	0.115 ^{NS}	-0.329 ^{NS}	0.037 ^{NS}	-5.202***	-0.038 ^{NS}	-0.022 ^{NS}	-0.038 ^{NS}	-0.022 ^{NS}	0.344**
Large ^a	1.458*	-0.178 ^{NS}	0.491 ^{NS}	0.491 ^{NS}	0.138*	0.138*	0.138*	-0.199*	-0.090 ^{NS}	-0.240***	-0.199*	-0.090 ^{NS}	-0.199*	-0.090 ^{NS}	-0.240***
Fresh ^a	1.090*	0.844*	2.451***	2.451***	-0.750***	0.063***	0.063***	-0.187**	-0.109 ⁺	-0.381***	-0.187**	-0.109 ⁺	-0.187**	-0.109 ⁺	-0.381***
Mod.d.	1.787 ^{NS}	2.054 ⁺	3.494*	3.494*	0.704*	-0.014 ^{NS}	-0.014 ^{NS}	0.704*	0.704*	-0.014 ^{NS}	-0.038*	-0.009 ^{NS}	-0.038*	-0.009 ^{NS}	-0.078***
Well-d. ^c	0.402 ^{NS}	-0.343 ^{NS}	-1.51**	-1.51**	0.255**	-0.024*	-0.024*	0.255**	0.255**	-0.024*	-0.001 ^{NS}	0.007 ^{NS}	-0.001 ^{NS}	0.007 ^{NS}	0.021***
Total ^a	0.090*	1.209 ⁺	0.928 ^{NS}	2.875**	0.095 ^{NS}	-0.003 ^{NS}	-0.003 ^{NS}	-0.199 ^{NS}	-0.242 ^{NS}	-0.935***	0.003 ^{NS}	0.018 ^{NS}	0.003 ^{NS}	0.018 ^{NS}	0.063***

The parameter estimates of the model are indicated with their *p* value. ****p* < 0.001; ***p* < 0.01; **p* < 0.05; †*p* < 0.10; ‡*p* < 0.100; †*p* < 0.100; ‡*p* > 0.100. The reference level for treatment was control. Fresh, including L-I and L-II decay classes; mod.d., moderately decayed, including L-III decay class; well-d., well-decayed, including L-IV and L-V decay classes; small, ≤20 cm diameter; large, >20 cm diameter

^a Square-root transformation

^b Clear-cut values were removed from the statistical analyses (close to 0)

^c Logarithmic transformation

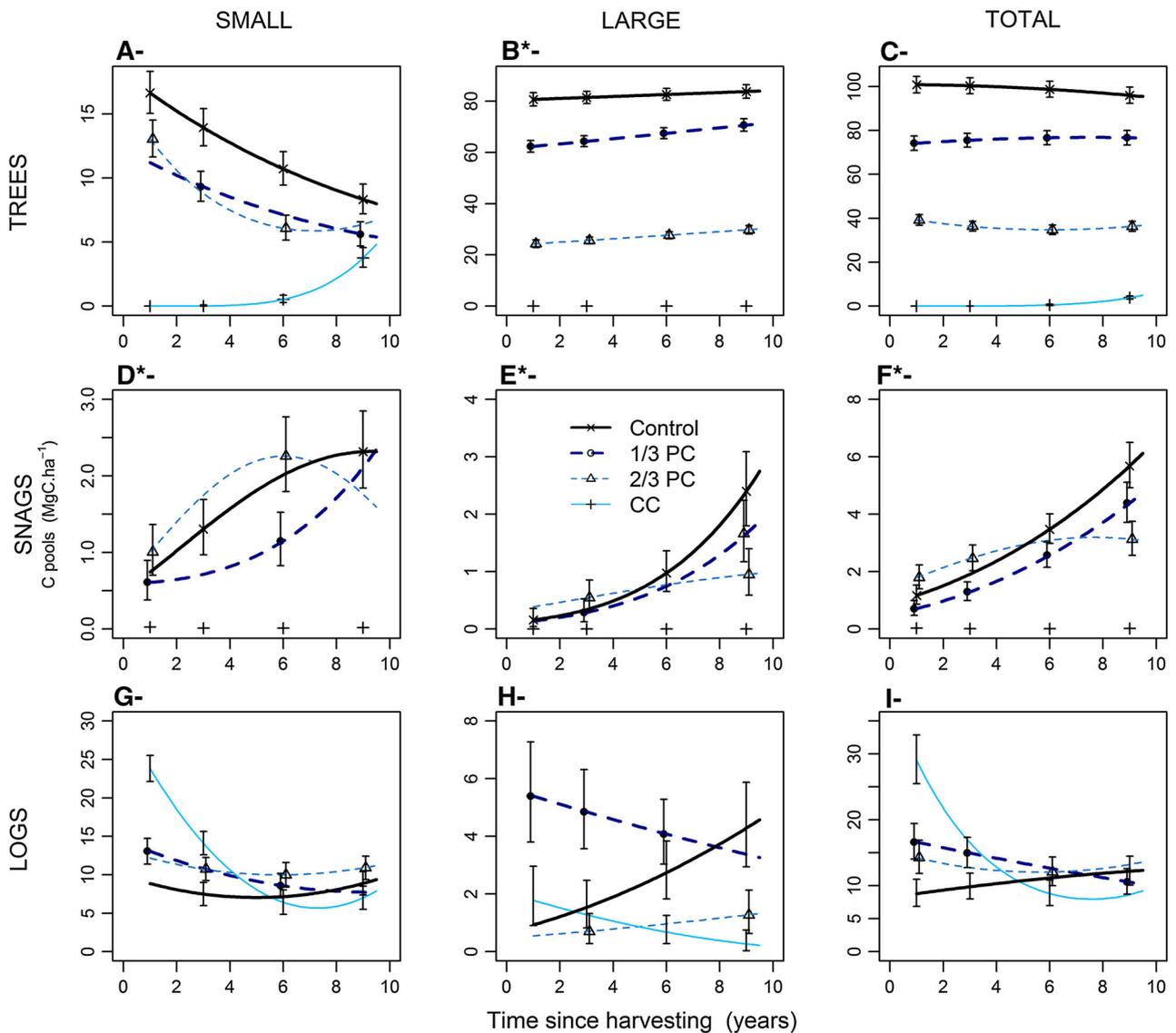


Fig. 3 Effects of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on aboveground C pools associated with **a** small, **b** large* and **c** total trees, with **d** small*, **e** large* and **f** total* snags, and with **g** small, **h** large and **i** total downed logs. *Note:* * Clear-cut

values are observed values, as they were removed from the statistical analyses (close to 0). Small, ≤ 20 cm diameter; large, >20 cm diameter

differences in tree biomass were still apparent (Fig. 5c). The composition of deadwood and snag C pools was very similar between the control and partial cut treatments, but following clear-cutting, there was a lower fresh log C pool, and no snags (Fig. 5c).

Discussion

Boreal mature aspen stands can sequester large quantities of C in aboveground tree biomass (Paré and Bergeron 1995). The $100.9 \text{ MgC ha}^{-1}$ that was reported for the 76-year-old control stands was within the range of values that were

found by Cavard et al. (2010) and Lee et al. (2002) for boreal mixedwood stands, and greater than values that have been reported for coniferous stands in the region (Cavard et al. 2010). In the study aspen stands, total tree biomass represented 64 % of C storage, while deadwood (snags and downed logs) C pools were similar to that of the forest floor, i.e. 11 %. The remaining C was stored in the mineral soil. Because we were interested in changes in soil C pools rather than their full quantification, our sampling was limited to the 0–10 cm mineral soil horizon. While the soil constitutes the dominant C pool in boreal stands (Lee et al. 2002; Martin et al. 2005), a large proportion of soil C is contained in the forest floor and surface mineral soil (Laganière et al. 2013).

Table 4 Effect of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on soil C pools in 1999 and in 2007, assessed by means of linear mixed models

Variable	One year following harvesting (1999)				Nine years following harvesting (2007)			
	Pre-harvest	1/3PC	2/3PC	CC	Pre-harvest	1/3PC	2/3PC	CC
Forest floor								
C pools	0.39***	3.173 ^{NS}	2.154 ^{NS}	7.329*	0.12 ⁺	3.314 ^{NS}	2.064 ^{NS}	5.596 ^{NS}
C pool in lignic FF						1.285 ^{NS}	−0.570 ^{NS}	3.219 ^{NS}
C pool in alignic FF						1.007 ^{NS}	1.365 ^{NS}	2.431 ^{NS}
C concentrations		−0.16 ^{NS}	−0.43 ^{NS}	4.70 ^{NS}		0.54 ^{NS}	0.19 ^{NS}	5.47 ^{NS}
C:N ratio		0.31 ^{NS}	1.17 ^{NS}	0.37 ^{NS}	0.19***	2.17 ^{NS}	0.07 ^{NS}	0.005 ^{NS}
Mineral soil (0–10 cm)								
C pools		2.955 ^{NS}	−0.103 ^{NS}	2.673 ^{NS}	−0.39*	−1.920 ^{NS}	−2.319 ^{NS}	6.322 ^{NS}
C concentrations	0.29***	0.385 ^{NS}	0.019 ^{NS}	0.051 ^{NS}		−0.161 ^{NS}	−0.218 ^{NS}	0.445 ^{NS}
C:N ratio	0.15**	−1.36 ^{NS}	−1.55 ^{NS}	−1.98 ^{NS}	0.14**	−0.72 ^{NS}	−0.04 ^{NS}	−1.07 ^{NS}

The parameter estimates of the model are indicated with their p value. *** $p < 0.001$; ** $0.001 < p < 0.010$; * $0.010 < p < 0.050$; $^{+}0.050 < p < 0.100$; ^{NS} $p > 0.100$. The reference level for treatment was control

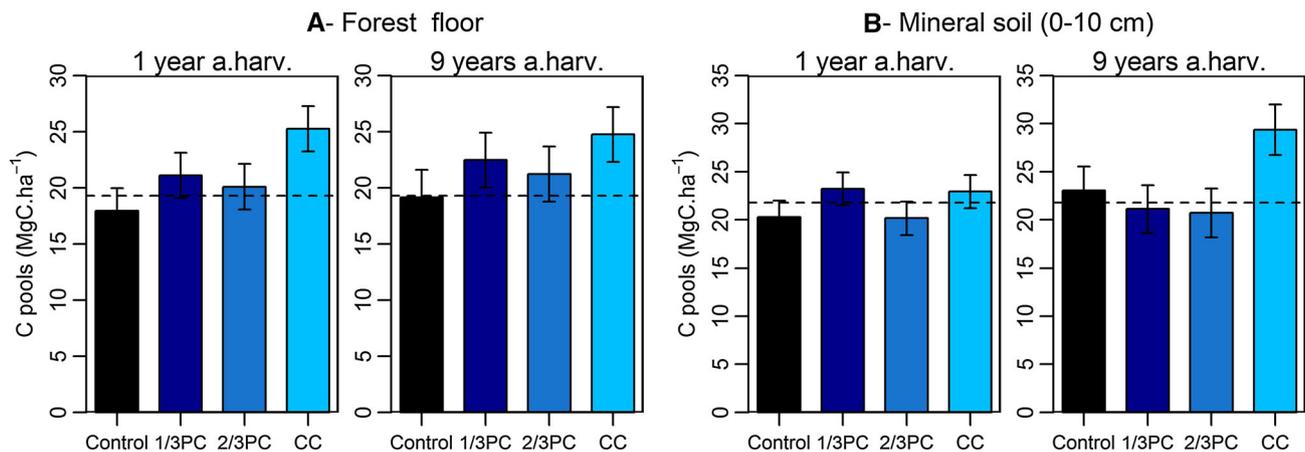


Fig. 4 Effects of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on C pools associated with **a** forest floor in 1999, and in 2007, and with **b** mineral soil (0–10 cm) in 1999, and in 2007.

Note: Broken line: average of variable before harvesting (1998), all sites and treatment confounded, used in models as covariable

This study provides a detailed examination of the mechanisms affecting stand C pools and fluxes over a 9-year period following partial and clear-cut harvesting in boreal aspen stands. We showed that the intensity of harvesting strongly controls C sequestration in biomass and C release from organic matter and, hence, the C balance of post-harvest stands. Compared to clear-cutting, partial harvesting maintained higher production of leaf litter and deadwood, and a larger snag C pool. It did not significantly affect decomposition, or forest floor and downed log C pools and chemical characteristics. Retention of residual stems following harvesting, even after a high degree of thinning, is an appropriate alternative to clear-cutting, while providing timber and maintaining a neutral C balance.

Effects of harvesting on carbon fluxes

Leaf litterfall

Increasing harvesting intensity and decreasing residual basal area resulted in an immediate decrease in C fluxes through leaf litterfall, as we expected in the first hypothesis. However, vigorous and abundant suckering of aspen following harvesting (Bourgeois et al. 2004; Brais et al. 2004) allowed for rapid re-establishment of foliar biomass (Liefers et al. 2002) and leaf litterfall recovered rapidly after partial cuts. Over time, the abundance of mountain maple (*Acer spicatum* Lamb.), which is a shade-tolerant high shrub species, increased in partial cuts and control stands

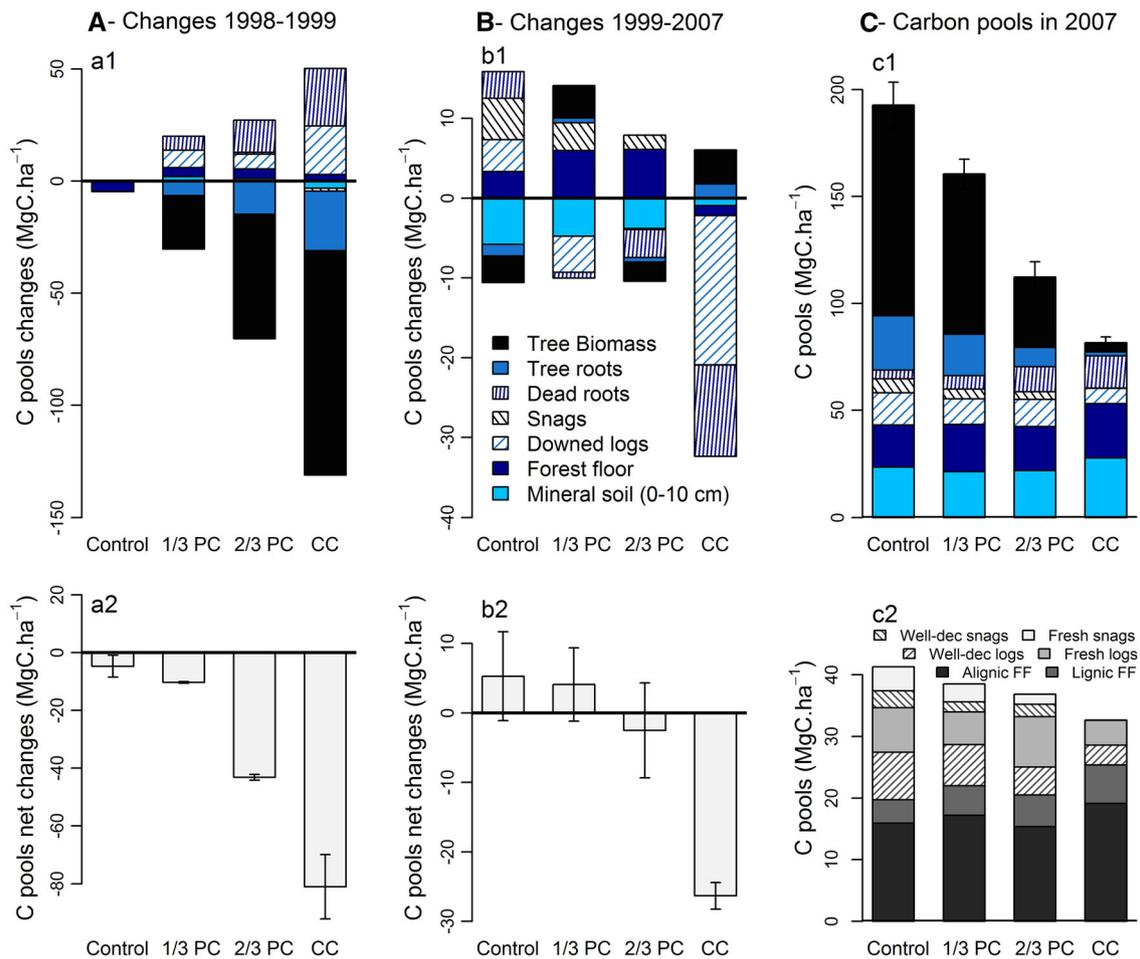


Fig. 5 Effect of partial cut (PC) and clear-cut (CC) harvesting of boreal aspen stands on C pools over a nine-year period following harvesting. **a** Net positive and negative changes between pre-harvest and post-harvest stand conditions (*a1*, individual C pools; *a2*, total C pools). **b** Net positive and negative changes between post-harvest stand condition and nine years following harvesting (*b1*, individual C pools; *b2*, total C pools). **c** Aboveground and belowground C pools

9 years after harvesting (*c1*, total C pools; *c2*, more details on dead organic matter C pools). *Note:* Fresh snags, including S-I and S-II decay classes; well-decayed (well-dec) snags, including S-III, S-IV and S-V decay classes; fresh logs, including L-I, L-II and L-III decay classes; well-decayed (well-dec) logs, including L-IV and L-V decay classes

(Bose et al. 2014b), contributing to deciduous litterfall. Nine years following clear-cutting, the C flux through leaf litterfall was half that of the control stands but never completely recovered to similar levels. Our third hypothesis was thus partly verified, but litterfall in clear-cut stands was bound to increase in subsequent years and reach values that were comparable to those of mature stands within a period of 15 years (Hughes and Fahey 1994). Such a rapid recovery has been observed in previous studies (Covington and Aber 1980; Hendrickson 1988; Lee et al. 2002).

Logging slash and tree mortality

High mortality rates of trees that were due to self-thinning accounted for most of the C flux from tree biomass to

deadwood C pools. An outbreak of forest tent caterpillar (*Malacosoma disstria* Hübner), which occurred in these stands in 2000, was responsible for the peak in aspen mortality that was observed between 2001 and 2004 in the control and partial harvesting treatments (Fig. 1; Bose et al. 2014a). As expected, a large transfer of C from tree branches and tops to the small log pool as logging slash was caused by on-site de-limbing during harvesting operations. Moreover, partial harvesting could have accelerated the mortality of residual trees through increased tree fall that was incurred by windthrow in post-harvest stands and through physical damage to residual stems during windthrow events (Bose et al. 2014a). The high C flux associated with mortality in the 2/3 partial cut was also a result of the harvesting prescription, which left mostly non-vigorous stems (Harvey and Brais 2007). Contrary to what

we expected in the second hypothesis, the production of deadwood following harvesting did not decrease relative to the undisturbed stands.

Harvesting also causes a large input of soil OM in the form of dead roots. Because aspen roots are prone to grafting and because aspen suckers can maintain the functioning of their parent root system for long period of time (DesRochers and Lieffers 2001a, b), our estimate of root mortality based on allometric equations might be much higher than actual mortality. Further studies are necessary to quantify root dynamics as well as root contributions to soil C after harvesting.

Decomposition of leaf litter and wood

Previous studies that were conducted in the same or similar stands of the region have reported minor effects of partial harvesting on microclimate (Brais et al. 2004), soil macrofauna (Brais et al. 2013), and the wood-decomposing fungal community (Kebli et al. 2012). This could explain the similar decomposition patterns that we observed between control and partially harvested stands, which were contrary to our third hypothesis. In a comparable study that was conducted in boreal mixedwood stands, Lee et al. (2002) also reported similar 3-year mass losses for aspen and balsam fir foliar litter in partial cut and control stands. Despite increased forest floor moisture following clear-cutting (Brais et al. 2004), decreases in decomposition rates of leaf litter and wood were observed. The lack of consistent responses of decomposition rates to canopy openings across studies (Prescott 1997; Wei et al. 1997; Hope et al. 2003; Shorohova et al. 2008) is an indication that factors other than soil moisture and temperature alter microbial dynamics and activity and thus decomposition.

Decomposition rates were similar between leaf litter and wood blocks of aspen. In a parallel study conducted in natural stands, Strukelj et al. (2012) reported higher proportions of highly recalcitrant waxes, cutins and lipids (Lorenz et al. 2007) in aspen leaves than in wood. Also, leaf litter has high concentrations of low molecular mass N compounds (e.g., ammonium and amino acids), as well as higher labile water-soluble constituents (e.g. sugars, amino acids and phenols) that are degraded more rapidly (Berg 2000). Aspen wood is characterised by a relatively high proportion of carbohydrates and low proportion of lignins (Strukelj et al. 2012), making it less resistant to decomposition. Leaf decomposition could lead to relatively higher accumulations of microbial products and concomitant stable soil organic matter formation (Cotrufo et al. 2013) and may form OM, which is more stable than that resulting from wood decomposition (Strukelj et al. 2012).

Effects of harvesting on carbon pools

Tree biomass

Carbon pools in tree biomass result from a tight balance between growth and mortality, which were both affected by harvest intensity (Bose et al. 2014a, b). The 1/3 partial cuts retained a much larger stock of carbon than the 2/3 partial cuts. As was performed in the 1/3 partial cut, thinning from below allowed for greater C sequestration in tree biomass, which was likewise reported by Hoover and Stout (2007). In the present study, relatively low C flux through mortality was observed in the 1/3 PC, which was attributable to the removal of non-vigorous stems during harvesting operations. Following both clear-cutting and 2/3 partial cuts, rapid regeneration of trembling aspen through suckering (Brais et al. 2004) hastened C accumulation in tree biomass. This process was likely to increase exponentially in subsequent years. Residual stem growth increased in the 2/3 partial cut, but not in the 1/3 partial cut (Bose et al. 2014a); this response did not compensate for initial high tree mortality in the 2/3 treatment and resulted in a decrease in its live biomass over the 9-year period. The C pools in tree biomass in clear-cut stands increased despite low net primary productivity that characterised young stands (Law et al. 2003). Nine years after harvesting, live tree biomass remained the pool that was most affected by treatments and decreased with increasing harvest intensity, consistent with expectation. In particular, the C pools in large trees were still strongly affected by treatments, in contrast to small trees, which resulted in a size class distribution of partially harvested stems that was close to the control stands.

Snags and downed logs

Over the study period, the 76-year-old control stands were characterised by the production of a large quantity of deadwood, especially in terms of high snag inputs. The absence of fresh logs in natural stands can be explained by the low occurrence of uprooting in aspen (Angers et al. 2010), combined with the rapid decay of downed aspen logs (Brais et al. 2006). Size class distributions of snags and downed logs in natural forests were fairly evenly distributed among small, and large size classes.

As expected, the size class distribution of downed logs after partial cutting approximated that of control stands. In clear-cuts, the distribution of downed logs was largely skewed towards small diameter classes, due to inputs of logging slash and the absence of tree mortality (Fraver et al. 2002; Pedlar et al. 2002). Because of their high surface to volume ratio (Fridman and Walheim 2000),

small logs that resulted from harvesting generally decomposed quickly (Pedlar et al. 2002; Moroni 2006). In the clear-cut treatment, small logs lost two-thirds of their mass within the initial 6 years that followed harvesting and reached C pools similar to those of the other treatments within 9 years. This response was consistent with estimates provided by the negative exponential decomposition model for wood blocks in the clear-cut treatment (Fig. 2). Rapid decomposition of small woody debris has also been reported for temperate hardwood forests (Mattson et al. 1987). However, in boreal coniferous forest, decomposition of small woody debris following clear-cutting may take more than 30 years (Moroni 2006; Hagemann et al. 2009).

Lower decay rates (k -values) have been reported for snags (0.027 year^{-1} , Angers et al. 2012b) than for logs (0.06 year^{-1} , Brais et al. 2006) of trembling aspen. By leaving standing dead trees and allowing for snag recruitment, partial cutting could promote C retention over the medium term. The C pool of logs recovered in all harvesting treatments, but the C pools of snags were reduced in harvesting treatments compared to the control. Further, the C fluxes that were incurred through tree mortality, 9 years after harvesting, were proportional to the residual basal areas. It is expected that with increased senescence mortality and stand break up, patterns of large snag and log accumulation in control stands will continue to diverge from those observed in harvested stands (Fig. 3e–h). Larger quantities of C would be stored in the deadwood component of control stands than in partial cuts (Powers et al. 2011).

Forest floor and upper mineral soil

Organic matter pools of the forest floor and mineral soil are controlled by the balance between C inputs through rhizodeposition, dead roots, leaf litter and deadwood, and the release of C through respiration and leaching (Jandl et al. 2007). The increase in the C pool in the forest floor immediately following clear-cutting could have resulted from the integration of some logging slash and well-decomposed logs that were crushed during harvesting operations (Brais et al. 2004). Nine years after clear-cut harvesting, the balance between the decrease in leaf litterfall, the input of logging slash and decreases in wood and leaf decomposition rates likely reduced the differences between clear-cuts and control stands. The recognised high spatial variability of C pools (Diochon et al. 2009) as indicated here by the large standard errors may have contributed to the lack of significant effects.

Mineral soil is a major C storage pool in boreal stands (Laganière et al. 2013), which is supplied by products of organic matter decomposition from forest floor and from root inputs. Increased leaching from the forest floor to the

mineral soil of dissolved organic C that was associated with lignin-derived compounds has been commonly reported following clear-cutting (Dai et al. 2001; Piirainen et al. 2002; Kalbitz et al. 2004). Leached C is transferred to the mineral soil, where it is largely retained and remains resistant to decomposition (Piirainen et al. 2002; Kalbitz et al. 2004). The forest floor of aspen stands is characterised by stable forms of soil organic C compared with other boreal species (Laganière et al. 2013); this may limit the effects of harvesting on the mineral soil C. Our results are consistent with those of Lee et al. (2002) for boreal mixedwood stands and with those reported by Zhou et al. (2013) following a meta-analysis of 81 partial cut experiments that were conducted in a range of forest types. The contribution of roots to soil C pools, through either decomposition of dead roots or rhizodeposition by live trees, needs further investigation.

Despite differences in the quantity and quality of litter inputs among the harvesting treatments, the C:N ratio of forest floor and mineral soil was not affected by harvesting treatment, contrary to what we expected. Likewise, Kranabetter and Coates (2004) found few effects of partial and clear-cutting with respect to the C:N ratio of mineral soil, but they observed a weak decrease in the C:N ratio of the forest floor. During litter decay, the preferential loss of easily degradable compounds (e.g. protein, starch, cellulose), the persistence of recalcitrant compounds (lignin, alkyl C compounds) and the formation of microbial products (Cotrufo et al. 2013) would ultimately lead to convergence in litter chemical composition (Wickings et al. 2012). All compounds would necessarily pass through the same physiological “funnel”, due to a limited set of biochemical pathways during decomposition (Fierer et al. 2009).

Effects of harvesting on stand carbon balance

As we hypothesised, the intensity of harvesting determined whether stands act as C sinks or sources. Following clear-cutting, stands became a C source, due to changes in the balance between net primary production and decomposition (Amiro et al. 2010). In contrast, following partial harvesting, residual stems maintain net primary productivity at levels that are sufficiently high to compensate for decomposition of logging slash. Consequently, stands in the 1/3 PC rapidly became a C sink. This has strong implications for management of forests for C sequestration.

Conclusion

Harvesting prescriptions have strong implications for residual stand structures and for the amount and nature of litter inputs in years following harvesting. Partial

harvesting allows for retention of C in live tree biomass and increased leaf and wood litter inputs when compared with clear-cutting. Partial harvesting also has a lower impact than clear-cutting on the decomposition dynamics of both wood and leaf litter. Live biomass, and snag and downed log C pools were the components that were most affected by the harvesting treatments. Both partial and clear-cut harvesting had no effect on soil C pools, indicating that the C of the forest floor and mineral soil is resistant to disturbance. Diversifying harvesting prescriptions could favour C sequestration at the ecosystem and landscape levels. This would be accomplished by maintaining live tree biomass stocks and sequestration potential, together with conserving high and continuous snag and large log inputs, which would decompose and become slowly integrated into the forest floor.

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