

# Forest carbon stocks in Newfoundland boreal forests of harvest and natural disturbance origin I: field study

M.T. Moroni, C.H. Shaw, and P. Otahal

**Abstract:** Quantification of stand and forest C stocks in response to different disturbances is necessary to develop climate change mitigation strategies and to evaluate forest C accounting tools. Live tree, dead tree, woody debris (WD), stump, buried wood, and organic and mineral soil C stocks are described in chronosequences of black spruce (*Picea mariana* (Mill.) BSP) (harvest and fire origin) and balsam fir (*Abies balsamea* (L.) Mill.) (insect and harvest origin). The largest C stocks were found in mineral soil ( $\leq 179 \text{ Mg}\cdot\text{ha}^{-1}$ ), organic soil ( $\leq 123 \text{ Mg}\cdot\text{ha}^{-1}$ ), and live tree ( $\leq 93 \text{ Mg}\cdot\text{ha}^{-1}$ ) pools. Live tree C changed predictably with disturbance history and time since disturbance, increasing with forest age. Regeneration growth slowed under snags. Thinning accelerated production of larger trees but reduced site live tree C. Dead tree and WD C were temporally dynamic and strongly influenced by disturbance history and time since disturbance, but abundances in differently disturbed forests converged at low levels 40–60 years after disturbance. Only immediately following natural disturbances were there large amounts of snag C ( $26\text{--}30 \text{ Mg}\cdot\text{ha}^{-1}$ ). WD C was relatively abundant <3 years after harvesting ( $15\text{--}17 \text{ Mg}\cdot\text{ha}^{-1}$ ) and 31–36 years after natural disturbance ( $9 \text{ Mg}\cdot\text{ha}^{-1}$ ). Buried wood stocks were small, but comparable with WD stocks in some forests.

**Résumé :** Il est nécessaire de quantifier les stocks de C dans les peuplements et les forêts en réaction aux différentes perturbations pour élaborer des stratégies visant à atténuer les effets des changements climatiques et pour évaluer les outils qui servent à mesurer le C des forêts. Les stocks de C dans les arbres vivants, les arbres morts, les débris ligneux (DL), les souches, le bois enfoui, le sol organique et le sol minéral sont décrits dans des chronoséquences d'épinette noire (*Picea mariana* (Mill.) BSP), issues de coupes et de feux, et des chronoséquences de sapin baumier (*Abies balsamea* (L.) Mill.) issues de coupes et d'épidémies d'insectes. Le sol minéral ( $\leq 179 \text{ Mg}\cdot\text{ha}^{-1}$ ), le sol organique ( $\leq 123 \text{ Mg}\cdot\text{ha}^{-1}$ ) et les arbres vivants ( $\leq 93 \text{ Mg}\cdot\text{ha}^{-1}$ ) contenaient les plus grandes quantités de C. Le C des arbres vivants variait de façon prévisible en fonction de la nature des perturbations et du temps écoulé depuis qu'est survenue une perturbation et il augmentait avec l'âge de la forêt. La croissance de la régénération ralentissait sous les chicots. L'éclaircie accélérât la production de plus gros arbres mais réduisait le C chez les arbres vivants qui restaient. Le C des arbres morts et des DL était temporairement dynamique et fortement influencé par la nature des perturbations et le temps écoulé depuis qu'est survenue une perturbation, mais l'abondance dans des forêts ayant subi différentes perturbations convergerait vers un faible niveau 40–60 ans après la perturbation. La quantité de C dans les chicots ( $26\text{--}30 \text{ Mg}\cdot\text{ha}^{-1}$ ) était élevée mais seulement immédiatement après une perturbation. Le C était relativement abondant dans les DL moins de 3 ans après une coupe ( $15\text{--}17 \text{ Mg}\cdot\text{ha}^{-1}$ ) et 31–36 ans après une perturbation naturelle ( $9 \text{ Mg}\cdot\text{ha}^{-1}$ ). La quantité de C dans le bois enfoui était faible mais comparable à la quantité de C dans les DL dans certaines forêts.

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## Introduction

The importance of Canada's forest resource to the global C cycle is being recognized, and efforts are being made to quantify the biomass resource and its C dynamics (e.g., Chen et al. 2000; Kurz et al. 2008, 2009). Forests contain large amounts of C in biomass, dead organic matter, and

soil and contribute to significant annual C exchanges with the atmosphere (Denman et al. 2007). This is especially true for boreal forest ecosystems that are now understood to play a critical role in the global C budget (Bradshaw et al. 2009). Collection of data quantifying C stocks of stands and forests is important for several reasons. It is required to support the development of forest management strategies aimed at de-

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creasing C sources and increasing C sinks (Canadell et al. 2007). These management strategies may, in part, be directed at reducing impacts of natural and anthropogenic disturbances to forests that have been shown to affect the source–sink relationship in forest ecosystems (Kurz et al. 2008; Running 2008). However, data comparing the effect of natural and anthropogenic disturbance history on forest C stocks, in particular dead organic matter and soil C, are limited. In addition, these data are needed to evaluate and develop forest C models that may be used to direct management and (or) policy decisions relevant to climate change mitigation and to estimate C stock and stock change for international reporting and potentially C accounting. In a companion paper to this study (Moroni et al. 2010), these data were used to evaluate such a model, the Carbon Budget Model of the Canadian Forest Sector 3 (Kurz et al. 2009).

The small-diameter dead wood characteristic of many boreal forests has different temporal dynamics than longer-lived forests with trees of larger diameters (Moroni 2006), such as those occurring in western and southern North America, where woody debris (WD) dynamics have been studied and documented for decades (Harmon et al. 2004). In contrast, the eastern and northern boreal is an enormous region, but there are relatively few comprehensive studies that include estimates for dead organic matter and mineral soil C pools in addition to the more commonly estimated tree biomass. Examinations of forest biomass dynamics have focused on one disturbance type (i.e., postharvest; Smith et al. 2009) and one stage of stand development (i.e., old growth; Thompson et al. 2003) or have been limited to specific dead organic matter pools such as snags (Smith et al. 2009) or dead wood (Moroni 2006). Consequently, there is a need to examine the impact of disturbance history and time since disturbance on a comprehensive set of biomass, dead organic matter, and soil C pools.

The objectives of the research reported here were to (i) quantify forest C stocks in two species of major economic and ecological significance in the North American boreal forest (black spruce (*Picea mariana* (Mill.) BSP) and balsam fir (*Abies balsamea* (L.) Mill.)) grown in Newfoundland and, in these forests, (ii) determine the impact of stand-replacing natural (insect and fire) and anthropogenic (harvesting) disturbances and precommercial thinning on C stocks, (iii) determine differences in forest C stocks with time since disturbance, and (iv) provide a comprehensive forest C data set to enable future evaluation of forest C models.

## Materials and methods

What follows is an overview of the field study, a general site description, and a summary of the study and sampling designs. For details, please refer to Moroni (2006).

The field study was conducted in Newfoundland, which represents the eastern extent of the Canadian Boreal Forest Region (Rowe 1972). The Newfoundland boreal forest is dominated by balsam fir and black spruce. Western Newfoundland receives prevailing moisture-laden westerly winds from the Gulf of St. Lawrence that bring 1000–1500 mm of annual precipitation. Prolonged dry periods and fire are absent in western Newfoundland, leading to conditions that pro-

mote forests dominated by balsam fir. In contrast, central Newfoundland is characterized by an inland, quasi-continental climate with warm, dry summers and a high fire danger (Wilton and Evans 1974). Frequent burning promotes forests dominated by black spruce in central Newfoundland.

The major anthropogenic disturbance in Newfoundland black spruce and balsam fir is clearcut harvesting; ~17 500 ha have been clearcut annually in recent years (Newfoundland Department of Forest Resources and Agriculture 1998). In addition, ~72 000 ha of Newfoundland fir were precommercially thinned between 1976 and 2005, and rates of precommercial thinning were recently ~2650 ha·year<sup>-1</sup> (Moroni 2006). The major natural disturbances in Newfoundland are fire in spruce forests (Wilton and Evans 1974) and insect outbreaks in fir forests (Hudak 1996).

Sites were selected to represent 12 populations of forests, hereafter strata, defined by the combination of dominant tree species (black spruce (S) or balsam fir (F)), a disturbance type (harvest (H), harvest with precommercial thinning (HT), burned (B), insect killed (I), or unknown origin (U)), and a stand age (young (Y), middle (M), or old (O)). Half of the strata were in fir and half in spruce. Three sampling sites were located for each stratum and four sampling plots were located at each sampling site for a total of 36 sites and 144 plots (Tables 1 and 2).

### Balsam fir dominated sites

The six strata (18 sites) in fir were located in western Newfoundland in forests of insect or harvest origin (Table 2). Because past disturbances have the potential to leave a legacy of dead wood within the current rotation, all young and middle-aged sites were selected where stands were mature to overmature fir-dominated forests at the time of the last stand-replacing disturbance and had regenerated or were regenerating to stands dominated by fir. Current and previous rotations were classified as good or medium yielding (for merchantable volume) (Table 2). This criterion could not be applied to the old-aged sites (F/U/O) where no records of previous stand types exist. Although large-scale forest harvesting began in the 1920s in western Newfoundland, accurate records of disturbance origin are only available from the 1960s, making it impossible to locate sites older than 50 years with known origins. Stands at old-aged sites were selected for study because they were likely to have originated following a stand-replacing insect outbreak, as they were even-aged sites that predated forestry activity, and fire typically does not occur in this region of Newfoundland. Tree species other than balsam fir encountered were black spruce, white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), red maple (*Acer rubum* L.), trembling aspen (*Populus tremuloides* Michx.), eastern larch (*Larix laricina* (Du Roi) K. Koch), American mountain-ash (*Sorbus americana* Marsh.), eastern white pine (*Pinus strobus* L.), and alternate-leaf dogwood (*Cornus alternifolia* L.f.).

Fifteen sites were located in central western Newfoundland near Corner Brook and Deer Lake and three near Plum Point on the Newfoundland northern peninsula (Table 2). Five of the strata were selected to represent two chronosequences (Table 2): one of insect-killed origin (F/I/Y–F/I/M–F/U/O) and the other of harvest disturbance origin (F/H/Y–

**Table 1.** Annotations used to describe strata and chronosequences of Newfoundland balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) sites.

| Annotation                    | Description   |
|-------------------------------|---|
| Species                       |   |
| F                             | Balsam fir  |
| S                             | Black spruce  |
| Disturbance history           |   |
| H                             | Harvested   |
| HT                            | Harvested and thinned   |
| B                             | Burned (wildfire)   |
| I                             | Insect  |
| U                             | Unknown   |
| Age class                     |   |
| Y                             | Young   |
| M                             | Medium  |
| O                             | Old   |
| Strata chronosequences        |   |
| F/I/Y–F/I/M–F/U/O             | Balsam fir stands of insect origin that are young and medium aged plus old-aged stands of unknown origin  |
| F/H/Y–(F/H/M or F/HT/M)–F/U/O | Balsam fir stands of harvested origin that are young and medium aged plus harvested and thinned medium-aged stands plus old-aged stands of unknown origin |
| S/H/Y–S/H/M–S/H/O             | Black spruce stands of harvested origin that are young, medium, and old aged  |
| S/B/Y–S/B/M–S/B/O             | Black spruce stands of fire origin that are young, medium, and old aged   |

F/H/M–F/U/O). Stand-replacing hemlock looper (*Lambdina fiscellaria* (Guenée)) outbreaks were the disturbance at the origin of insect-killed sites (F/I/Y and F/I/M) that were not salvage logged. Harvesting removed all softwood stems with diameter at breast height (DBH)  $\geq 9$  cm to a top diameter of 8 cm. The sixth stratum (F/HT/M) was added to evaluate the impact of precommercial thinning on C, particularly with regard to live and dead wood dynamics. Thinned sites were paired with unthinned harvested sites of the same stand age (M). Thinned sites were precommercially thinned 8–20 years before measurement. Thinned sites were reduced from an unknown original stocking to  $\sim 2000$  stems $\cdot$ ha $^{-1}$ . Thinning targeted smaller, nonmerchantable, and sick or damaged trees, leaving thinned stems where they fell.

### Black spruce dominated sites

The six strata (18 sites) in black spruce were located in central Newfoundland in forests of fire or harvest origin (Table 2). All sites were located near or to the west of Grand Falls-Windsor, Newfoundland. As with the balsam fir sites, every attempt was made during the site selection process to avoid the potential legacy of dead wood within the current rotation from past disturbances by selecting for sites where the stands were mature to overmature spruce-dominated forests at the time of the last stand-replacing disturbance and had regenerated or were regenerating to stands dominated by spruce. Current and previous rotations were classified as good or medium yielding for merchantable volume (Table 2). All sites selected met these criteria except for the old-aged stands for the same reason given for old-aged balsam fir sites and except for one of the three replicate sites for S/H/M in which the previous rotation was of poor, rather than medium or high, yield. Tree species other than black spruce encountered were balsam fir, white birch, eastern white pine, and trembling aspen.

The strata were selected to form two chronosequences: one of harvest origin (S/H/Y–S/H/M–S/H/O) and one of fire origin (S/B/Y–S/B/M–S/B/O) (Table 2). All fires were stand replacing and were not salvage logged. Harvesting removed all stems of DBH  $\geq 9$  cm to a top diameter of 6 cm.

### Sampling design

All field measurements in fir were conducted from June to September 2003 and in spruce from June to September 2004. The plot design and field measurements were based on the National Forest Inventory Ground-plot Protocol (Natural Resources Canada 2009). Four sample plots were located randomly within each site. Each plot comprised two concentric circular subplots (radius 11.28 and 3.99 m, respectively) with two 40 m line transects, perpendicular to each other, crossing at their midpoint at the plot center. At the end of one randomly selected transect, a circular subplot (radius 0.56 m) was established.

Diameter and height of live trees and snags with DBH  $\geq 9$  cm were measured within the 11.28 m radius circular subplot. Diameter and height of live trees and snags with DBH  $< 9$  cm and height and top diameter of stumps (rooted bole portion of dead trees that were  $< 1.3$  m tall) were measured within the 3.99 m radius circular subplot. Live tree aboveground biomass was estimated from published regression equations based on height and DBH (Young et al. 1980; Lavigne 1982; Crow and Erdmann 1983; Alemdag 1984; Ter-Mikaelian and Korzukhin 1997). Belowground biomass was estimated using relationships between above- and belowground biomass developed by Li et al. (2003) where the relationship for softwoods was also applied to hardwoods. The relationships for estimating hardwood root biomass in Li et al. (2003) are not appropriate for estimating the biomass of roots when few trees dominated by large-dimension hardwoods survive disturbances. Live tree C stocks

**Table 2.** Range of values for the characteristics of Newfoundland balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) sites studied.

| Lead species/<br>disturbance history/<br>stand age class <sup>a</sup> | Years of last<br>disturbance <sup>b</sup> | Current forest<br>type <sup>a,c</sup> | Current forest<br>age (years) <sup>b,d</sup> | Previous forest<br>type <sup>c,e</sup> | Previous forest age<br>(years) when<br>disturbed <sup>d,f</sup> | Mean annual<br>temperature<br>(°C) <sup>e,g</sup> | Precipitation<br>(mm·year <sup>-1</sup> ) <sup>e,g</sup> | Elevation (m) |
|---|---|---------------------------------------|--|--|---|---|--|---------------|
| <b>Balsam fir</b>   |   |                                       |  |  |   |   |  |               |
| F/I/Y   | 2000–2001                                 | na                                    | na   | bf 2 M                                 | 60–66   | 1.7   | 1103–1104  | 45            |
| F/I/M   | 1966–1971                                 | bf 2 M–G                              | 30   | bf 1–2 M                               | 96–136  | 4.2–4.4   | 1380–1393  | 65            |
| F/H/Y   | 2002–2003                                 | na                                    | na   | bf 1–2 M                               | 60–95   | 2.8–3.0   | 1112–1318  | 255–325       |
| F/H/M   | 1962–1971 <sup>g,h</sup>                  | bf 2 M–G                              | 32–36  | bf 2 M                                 | 102–111   | 3.3–3.9   | 1023–1479  | 105–280       |
| F/HT/M <sup>i</sup>   | 1962–1971 <sup>g,h</sup>                  | bf 1–2 M–G                            | 32–36  | bf 2 M                                 | 102–111   | 3.3–3.9   | 1023–1479  | 105–280       |
| F/U/O   | 1894–1917                                 | bf 2 G                                | 86–109                                       | na                                     | na  | 2.6–2.7   | 1437–1468  | 435–445       |
| <b>Black spruce</b>   |   |                                       |  |  |   |   |  |               |
| S/B/Y   | 2002–2004                                 | na                                    | na   | bs 2 M                                 | 62–75   | 3.3–3.4   | 1122–1211  | 145–217       |
| S/B/M   | 1970                                      | bs 2–3 M                              | 31   | bs 1 M                                 | 76  | 3.3   | 1215–1217  | 219–231       |
| S/B/O   | 1930 <sup>g,h</sup>                       | bs 1–2 M                              | 68–92  | na                                     | na  | 3.2–3.3   | 1151–1279  | 99–194        |
| S/H/Y   | 2001–2002                                 | na                                    | na   | bs 1–3 M–G                             | 71–72   | 3.3   | 1139–1143  | 60–99         |
| S/H/M   | 1965–1970                                 | bsbf 1–2 M                            | 31–36  | bsbf 2–3 P–M                           | 85–136  | 3.4   | 1127–1197  | 175–248       |
| S/H/O   | 1930 <sup>g,h</sup>                       | bs 2–3 M                              | 63–72  | na                                     | na  | 3.3   | 1150–1158  | 99–108        |

**Note:** na, data not available or applicable.

<sup>a</sup>Lead species: black spruce (S), balsam fir (F); disturbance history: insect killed (I), harvested (H), harvested with precommercial thinning (HT), origin unknown (U); stand age class: young aged (Y), middle aged (M), old aged (O).

<sup>b</sup>Stand age was substituted for year of disturbance in old-aged stands where disturbance origin is not known.

<sup>c</sup>Newfoundland forest inventory of current forest; forest inventory (ab A B) where bf = >75% balsam fir, bs = >75% black spruce, bsbf = 50%–75% black spruce, 25%–50% balsam fir. A = crown density where 1 is over 75% crown closure, 2 is 51%–75% crown closure, and 3 is 26%–50% crown closure; B is site class (for merchantable yield) where M is medium and G is good. Growth and yield curves for a site type on the northern peninsula are slightly lower than for the same site type in central western Newfoundland (Newfoundland and Labrador Department of Natural Resources, 2005. Unpublished Newfoundland forest growth curves).

<sup>d</sup>Forest age at measurement or age of forest disturbed within 3 years of measurement. Forest ages determined from increment bore or stump ring count.

<sup>e</sup>Newfoundland forest inventory for forests disturbed within 3 years of measurement. Aerial photographs were typed to determine previous forests in stands disturbed >3 years of measurement.<sup>c</sup>

<sup>f</sup>Forest age was determined from increment bore or stump ring count where forests were disturbed within 3 years of measurement. Previous forest ages in sites disturbed >3 years before measurement were estimated from aerial photographs.

<sup>g</sup>Averages for the period 1971–2000 using estimates of McKenney et al. (2001).

<sup>h</sup>The exact year of disturbance is unavailable for some sites.

<sup>i</sup>Age when thinned 14–20 years.

were estimated by multiplying live tree oven-dry biomass by 0.5. Snag volume was estimated by determining dead wood volume from published equations based on height and DBH. Stump volume was estimated from stump height and top diameter. Snag and stump biomasses were estimated by assigning decay classes to dead wood densities (Moroni 2006; Natural Resources Canada 2009). Carbon stocks of snags and stumps were estimated by multiplying biomass by 0.5. For a more detailed description of snag, stump, and WD estimation, see Moroni (2006).

WD diameters were measured at their point of intersection along the 40 m transects. WD volumes were calculated using the line intersect method (Marshall et al. 2000, eq. 8) and biomass was estimated by assigning decay classes to dead wood densities. WD <1 cm in diameter was estimated from the dry mass of <1 cm WD collected in the 0.56 m radius plots (Moroni 2006).

Thicknesses of the organic soil horizons and buried dead wood were measured at 2 m intervals along each 40 m transect. At each interval, a shovel was driven into the ground to measure the thickness of the organic horizons or buried wood. Buried wood was measured if it was more than half buried in the organic horizons or if encountered in the top 2 cm of the organic horizons. The area of the plot occupied by buried wood or organic horizons was determined from the proportion of 2 m observations that encountered these tissues. The volume of buried wood or soil organic horizons was estimated from the average thickness of each multiplied by the area that they occupied in the plot. Volume of buried wood was multiplied by species- and decay-class-specific densities (Moroni 2006) to estimate buried wood biomass. Half of the buried wood biomass was assumed to be C. Organic horizon bulk density was estimated from the volume and oven-dry mass of a sample taken from a 20 cm × 20 cm area to the top of the mineral soil in the 0.56 m radius circular plot. Organic horizon samples were dried at 55 °C for 4 days, subsampled, and passed through an 850 µm mesh before C analysis using a LECO CNS-2000 (LECO Corporation, St. Joseph, MI) combustion analyzer following the method of Leco Corporation (2003).

From each site, 0.75–1.5 dm<sup>3</sup> mineral soil samples, which included coarse fragments (>2 mm in diameter), were taken from 0–15, 15–30, and 30–45 cm depths. Depth samples were taken from all four plots at 0–15 cm, from two randomly selected plots at 15–30 cm, and from one randomly selected plot at 30–45 cm. The volume of each hole excavated during soil sampling was measured by placing a plastic bag in the hole and measuring the volume of glass beads required to fill the hole. Mineral soil samples were air-dried and passed through a 2 mm mesh, dried at 55 °C for 4 days, and weighed. Bulk density of <2 mm mineral soil was estimated based on <2 mm dry mass and the volume excavated. A subsample of <2 mm mineral soil was passed through an 850 µm mesh before C analysis using a LECO CNS-2000 combustion analyzer following the method of Leco Corporation (2003).

### Statistical analyses

Carbon stock data were highly skewed; no specific transformations could adequately normalize data for standard parametric techniques. Permutation tests, procedures using

multiple random resamplings of data, were used to establish group differences for C stocks within and between strata. For each test, 20 000 resamplings were performed and the *F* statistic was used to determine an approximate *p* value (Edgington 1995). The results are analogous to one-way analysis of variance, without requiring the standard distributional and variance assumptions. Fisher's protected least significant difference post hoc test on the resampled data was used to establish specific pairwise differences (Westfall and Young 1993). Carbon pools between thinned and unthinned fir were not severely skewed and were compared separately using a standard paired *t* test. All statistical analyses were conducted using R 2.8.1. (R Development Core Team 2008).

### Results

The largest forest C stocks were found in the mineral soil (up to 179 Mg·ha<sup>-1</sup>), organic soil horizon (up to 123 Mg·ha<sup>-1</sup>), and live tree (up to 93 Mg·ha<sup>-1</sup>) components (Table 3). Within half the strata, mineral soil was the largest C pool and no pool contained significantly more C than mineral soil in any strata. In three fir strata and three spruce strata, soil organic horizon C stocks were among the highest forest C pools. However, there were no clear trends for soil C with increasing stand age. In the old-aged strata (F/U/O, S/H/O, and S/B/O) and in F/HT/M, the C content of live trees was among the highest forest C stocks. Stumps contained the lowest C stocks (<2 Mg·ha<sup>-1</sup>) for all but the most recent and middle-aged harvested strata (F/H/Y, F/HT/M, S/H/Y, and S/H/M). Buried wood (1–6 Mg·ha<sup>-1</sup>) was also among the lowest C stocks in older spruce (S/B/O and S/H/O), middle-aged harvested fir (F/H/M), and middle-aged burned spruce (S/B/M) whereas snags were among the lowest C stocks in recently harvested (F/H/Y and S/H/Y), thinned (F/HT/M), and middle-aged burned spruce (S/B/M) strata (0.0–0.4 Mg·ha<sup>-1</sup> in these strata). Carbon stocks in the dead tree pools were also low (0–11 Mg·ha<sup>-1</sup>) in all strata except for those most recently naturally disturbed (26–30 Mg·ha<sup>-1</sup>; F/I/Y and S/B/Y). Carbon stocks in WD were generally low (3–10 Mg·ha<sup>-1</sup>) for all strata except recently harvested strata, middle-aged thinned fir, and middle-aged naturally disturbed strata (5–17 Mg·ha<sup>-1</sup>; F/H/Y, S/H/Y, F/HT/M, F/I/M, and S/B/M). Live tree C stocks were low in recently harvested (0–2 Mg·ha<sup>-1</sup>; F/H/Y and S/H/Y) and naturally disturbed (2–11 Mg·ha<sup>-1</sup>; F/I/Y and S/B/Y) strata.

### Live tree

The C content of total live trees and live trees with ≥9 cm DBH tended to increase with forest age in fir and spruce (Table 3). However, the temporal dynamics of the <9 cm DBH trees differed from the ≥9 cm DBH trees. The largest C content of <9 cm DBH live trees in fir occurred in middle-aged strata regardless of disturbance origin (30–42 Mg·ha<sup>-1</sup>; F/H/M and F/I/M) (Table 3). The pattern was similar for spruce of harvest origin (34 Mg·ha<sup>-1</sup> of <9 cm DBH trees in S/H/M) (Table 3), but for spruce of fire origin, the C content of <9 cm DBH live trees increased from the young to the middle-aged strata, which was equivalent to the old burned strata (20–28 Mg·ha<sup>-1</sup>; S/B/M and S/B/O) (Table 3). Medium-aged harvested thinned (F/HT/M) and unthinned fir

**Table 3.** Carbon content (Mg·ha<sup>-1</sup> with SE in parentheses) of the balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) sites studied.

|                                    | Balsam fir stratum     |                        |                       |                        |                        |                       | Black spruce stratum |                       |                       |                       |                       |                      |
|------------------------------------|------------------------|------------------------|-----------------------|------------------------|------------------------|-----------------------|----------------------|-----------------------|-----------------------|-----------------------|-----------------------|----------------------|
|                                    | F/I/Y                  | F/H/Y                  | F/I/M                 | F/H/M                  | F/U/O                  | F/HT/M                | S/B/Y                | S/H/Y                 | S/B/M                 | S/H/M                 | S/B/O                 | S/H/O                |
| Live trees                         |                        |                        |                       |                        |                        |                       |                      |                       |                       |                       |                       |                      |
| Hardwood                           | 2.7 (0.9)              | 2.2 (0.8)              | 7.8 (0.5)             | 6.4 (3.0)              | 7.4 (2.0)              | 1.1 (1.0)             | 0.0 (0.0)            | 0.0 (0.0)             | 0.2 (0.1)             | 0.1 (0.1)             | 2.7 (2.1)             | 7.0 (4.9)            |
| Softwood                           | 1.6 (0.8) a            | 0.0 (0.0) a            | 29.9 (4.1) b          | 42.1 (6.5) b           | 0.7 (0.4) a            | 0.8 (0.6)**           | 0.0 (0.0) a          | 0.1 (0.1) a           | 28.0 (2.9) c          | 33.6 (4.2) c          | 19.5 (9.8) bc         | 14.9 (5.0) b         |
| DBH <9 cm total                    |                        |                        |                       |                        |                        |                       |                      |                       |                       |                       |                       |                      |
| Softwood                           | 9.6 (3.8) ab           | 2.5 (0.4) a            | 10.3 (2.1) b          | 29.3 (10.2) b          | 84.6 (6.0) c           | 55.5 (2.7)*           | 1.9 (1.9) ab         | 0.0 (0.0) a           | 0.6 (0.3) a           | 6.3 (1.9) b           | 73.2 (24.7) c         | 76.8 (9.7) c         |
| DBH ≥9 cm total                    |                        |                        |                       |                        |                        |                       |                      |                       |                       |                       |                       |                      |
| Live tree total                    | <b>11.2 (4.4) aC</b>   | <b>2.5 (0.4) aB</b>    | <b>40.3 (4.6) bD</b>  | <b>71.4 (13.8) cD</b>  | <b>85.3 (5.7) cE</b>   | <b>56.3 (2.8) E</b>   | <b>1.9 (1.9) aAB</b> | <b>0.1 (0.1) aA</b>   | <b>28.6 (3.1) bC</b>  | <b>39.9 (6.1) bD</b>  | <b>93.2 (15.0) cD</b> | <b>91.7 (8.1) cE</b> |
| Dead organic matter                |                        |                        |                       |                        |                        |                       |                      |                       |                       |                       |                       |                      |
| Snags                              | <b>30.2 (1.0) dD</b>   | <b>0.4 (0.1) aA</b>    | <b>1.7 (0.3) bB</b>   | <b>1.9 (0.4) bB</b>    | <b>11.3 (2.3) cC</b>   | <b>0.0 (0.0) A**</b>  | <b>26.1 (5.1) cC</b> | <b>0.0 (0.0) aA</b>   | <b>0.1 (0.1) aA</b>   | <b>0.1 (0.0) aA</b>   | <b>3.6 (1.7) bB</b>   | <b>1.3 (0.5) bB</b>  |
| Stumps                             | <b>0.6 (0.3) bcA</b>   | <b>1.8 (0.7) cB</b>    | <b>0.1 (0.1) abA</b>  | <b>0.6 (0.1) bcA</b>   | <b>0.1 (0.0) aA</b>    | <b>0.6 (0.2) B</b>    | <b>0.1 (0.0) aA</b>  | <b>1.6 (0.2) dB</b>   | <b>0.1 (0.0) bA</b>   | <b>0.5 (0.2) cB</b>   | <b>0.1 (0.0) abA</b>  | <b>0.2 (0.1) bcA</b> |
| Woody debris                       | <b>4.4 (0.4) aC</b>    | <b>16.6 (4.3) bC</b>   | <b>9.3 (1.2) bC</b>   | <b>4.2 (0.3) aC</b>    | <b>10.1 (1.2) bC</b>   | <b>5.6 (1.7) C</b>    | <b>2.5 (1.2) aB</b>  | <b>15.1 (1.7) cC</b>  | <b>9.4 (1.8) bB</b>   | <b>2.6 (0.3) aC</b>   | <b>4.9 (2.5) abB</b>  | <b>3.7 (1.0) aC</b>  |
| Buried wood                        | <b>2.5 (0.8) B</b>     | <b>5.8 (3.4) B</b>     | <b>2.7 (0.7) B</b>    | <b>1.7 (0.6) AB</b>    | <b>2.3 (1.1) B</b>     | <b>4.3 (1.3) C</b>    | <b>2.8 (1.3) B</b>   | <b>1.1 (0.5) B</b>    | <b>3.9 (2.2) A</b>    | <b>2.6 (1.0) C</b>    | <b>1.3 (1.3) AB</b>   | <b>1.0 (0.6) AB</b>  |
| Soil organic horizons              | <b>123.3 (31.1) cE</b> | <b>31.0 (5.3) aC</b>   | <b>43.0 (8.7) abD</b> | <b>38.5 (12.5) abD</b> | <b>48.0 (1.0) bD</b>   | <b>35.0 (6.7) D</b>   | <b>50.4 (9.4) D</b>  | <b>43.6 (4.2) D</b>   | <b>60.5 (10.0) D</b>  | <b>34.1 (2.0) D</b>   | <b>45.5 (3.0) C</b>   | <b>43.5 (4.5) D</b>  |
| Soil mineral horizons <sup>a</sup> | <b>178.8 (42.4) cE</b> | <b>65.5 (12.0) abD</b> | <b>49.1 (11.3) aD</b> | <b>52.9 (5.2) aD</b>   | <b>97.2 (11.6) bcE</b> | <b>88.0 (11.4) F*</b> | <b>74.0 (18.2) D</b> | <b>104.2 (40.5) D</b> | <b>100.3 (23.8) D</b> | <b>136.3 (31.3) E</b> | <b>104.5 (19.3) D</b> | <b>97.0 (8.6) E</b>  |
| Ecosystem total                    | 351.0 (59.9) c         | 123.7 (7.1) a          | 146.2 (23.5) ab       | 171.3 (11.1) b         | 254.1 (6.8) bc         | 189.9 (13.2)          | 157.8 (26.7)         | 164.8 (39.8)          | 202.9 (32.9)          | 216.2 (33.5)          | 253.1 (31.9)          | 238.4 (10.9)         |

**Note:** Lowercase letters denote differences ( $p < 0.05$ ) within rows (excluding F/HT/M), uppercase letters denote differences ( $p < 0.05$ ) between bolded numerals within columns and tree species, and asterisks denotes differences (\*\* $p < 0.05$  and \* $p < 0.1$ ) between F/HT/M and F/H/M only ( $n = 3$ ). Hardwood pools were not compared due to a high incidence of no hardwood biomass within sites. See Table 2 for description of strata annotations.

<sup>a</sup>0–45 cm depth.

(F/H/M) contained equivalent amounts of live tree C (56–71 Mg·ha<sup>-1</sup>). However, the thinned strata (56 Mg·ha<sup>-1</sup>) contained significantly more ≥9 cm live tree C than the unthinned strata (29 Mg·ha<sup>-1</sup>) but less <9 cm live tree C than unthinned fir of a similar age (F/H/M) (Table 3). Old-aged fir (F/U/O) contained 11.3 Mg dead tree C·ha<sup>-1</sup> and 0.7 Mg C·ha<sup>-1</sup> in live trees with DBH <9 cm, indicating that stand breakup and replacement with a cohort of regenerating trees was in progress.

In general, live tree hardwood C stocks constituted a relatively small proportion of total live tree C. Hardwoods comprised larger proportions of live tree C in fir-dominated forests than in spruce-dominated forests (Table 3). Carbon stocks of live hardwood trees tended to increase with stand age in both spruce- and fir-dominated forests. In spruce, the proportion of live tree C stocks in hardwoods tended to increase with stand age; however, in fir, it ranked highest in recently disturbed strata (F/I/Y and F/H/Y).

### Dead wood

Snags were minor C pools in all but recently naturally disturbed strata (F/I/Y and S/B/Y) (Table 2). These strata were characterized by high C stocks in the snag pool (26–30 Mg·ha<sup>-1</sup>) and low C stocks in the WD pool (3–4 Mg·ha<sup>-1</sup>) (Table 3) whereas the opposite was true (0–2 Mg snag C·ha<sup>-1</sup> and 9 Mg WD C·ha<sup>-1</sup>) for middle-aged forests originating from the same natural disturbances (Table 2). This suggests that natural disturbances generated large amounts of snag C, but by the time these forests reach middle age, almost all snags have transferred to WD pools. Although snag C content is low in middle- and old-aged fir, a trend exists for it to increase from middle- to old-aged forests, and middle-aged thinned harvested fir (F/HT/M) contained less snag C than middle-aged unthinned fir (F/H/M).

Snag and WD C dynamics of stands originating from the anthropogenic disturbance of harvesting differed significantly from those described for natural disturbances (burned and insect killed). Recently harvested strata (F/H/Y and S/H/Y) contained the largest amounts of WD C (15–17 Mg·ha<sup>-1</sup>) compared with all other strata. The C content of WD was significantly lower in middle-aged harvested strata (3–4 Mg·ha<sup>-1</sup>) compared with the recently harvested strata. Within chronosequences, WD C stocks in unthinned middle-aged harvested strata (F/H/M and S/H/M) were low (2–3 Mg·ha<sup>-1</sup>) whereas unthinned middle-aged fir F/H/M contained about half of the WD C stocks of thinned fir strata at a similar stand age (6 Mg·ha<sup>-1</sup>; F/HT/M). WD C stocks were minor in all old-aged spruce strata regardless of disturbance origin. The WD C stock in old-aged fir was similar to that in middle-aged fir of insect-killed origin and higher than that in middle-aged fir of harvest origin (Table 3).

Stump and buried wood C stocks were low, with <2 Mg stump C·ha<sup>-1</sup> and 1–6 Mg buried wood C·ha<sup>-1</sup> across all strata (Table 3). The most recently harvested strata contained the largest amount of stump C. Buried wood contained up to 112% of the C found in WD and estimates of buried wood C were conservative, as dead wood buried entirely below 2 cm in the organic horizons was not recorded. Organic horizon thickness averaged 11 cm under fir and

9 cm under spruce and was therefore sufficiently thick to cover several size classes of WD.

### Organic and mineral soil and total ecosystem C stocks

For spruce, there were no significant differences between strata for mineral soil, organic soil, or total ecosystem C stocks. For fir, there was no trend in organic or mineral soil C with disturbance history or forest age, but there were some differences between strata (Table 3). The recently insect-killed stratum (F/I/Y) (Table 3) contained the largest amounts of organic and mineral soil C followed by the old-aged fir (F/U/O). The remaining young stratum (F/H/Y) had the lowest organic and mineral soil C stocks and the middle-aged strata (F/H/M and F/I/M) had mineral soil (31–43 Mg·ha<sup>-1</sup>) and organic horizon (49.1–65.5 Mg·ha<sup>-1</sup>) C stocks that were not significantly different from one another.

For fir, total ecosystem C stocks ranked highest in recently insect-killed fir (F/I/Y), which contained more total C than the recently harvested stratum (F/H/Y) and middle-aged strata (F/I/M and F/H/M), but had equivalent total C stocks to those of older fir (F/U/O). The lowest total C stocks were located in recently harvested (F/H/Y) and middle-aged (F/I/M and F/H/M) strata.

## Discussion

### Live tree

Live tree C was in the upper range reported for the boreal forest where 0.8 and 118.7 Mg C·ha<sup>-1</sup> was reported for Alaskan black spruce and Russian Scots pine (*Pinus sylvestris* L.) forests, respectively (Gower et al. 2001). Estimates for black spruce stemwood C from this study were very similar to those reported for Canadian boreal black spruce by Chertov et al. (2009). Measured live tree C tended to increase with forest age, although the data suggest the onset of senescence in the old-aged fir (F/U/O) and in the 92-year-old spruce strata regenerated following fire (S/B/O) (Table 3) (Moroni 2006). Senescence was indicated by large amounts of snags and a cohort of <9 cm live trees. Significant senescence in forests aged 86–109 years (Tables 2 and 3) deviates from growth expectations described by yield curves for these forest types where yield curves do not project significant senescence until forests are >115 years old (Newfoundland and Labrador Department of Natural Resources. 2005. Unpublished Newfoundland forest growth curves).

The middle-aged naturally disturbed stands (F/I/M and S/B/M) contained significantly less live tree C than the middle-aged harvested stands (F/H/M and S/H/M) (Table 3). In fir, this may be the result of slowed regeneration of the insect-killed stand because dense regeneration, undamaged by harvesting machinery, may have slowed regeneration growth (e.g., Piene 1981), but this effect is less likely in less dense spruce regeneration (Karsh et al. 1994). Recent evidence suggests that the shading effect of snags left standing following natural disturbances slows the growth of regeneration. Crown openness (percent sky visible through crowns), indicative of light transmission through crowns, was 9% for live balsam fir, 45% when snags retained branches and twigs, 68% when crowns had lost most smaller branches, and 90% with only large branches retained (K.D. Coates, J. Poulin, C. Messier, and J. Barte-

mucci, unpublished data), with similar trends observed for a range of species. Reductions in light transmittance reduce diameter and height growth (Coates and Burton 1999) and <75% open photosynthetic light intensity delays the transfer of balsam fir advanced regeneration dominance from lateral branches to apical leaders (Duchesneau et al. 2001), slowing the growth of regeneration under snags. Thus, regeneration following natural disturbances where snags are retained (F/I/M and S/B/M) is likely to grow slower than in disturbed landscapes where snags are removed, such as harvesting (F/H/M and S/H/M) or natural disturbances followed by salvage logging. Differences in forests growth attributable to variables such as shading or disturbance history are not accounted for in yield curves assigned to forests based on interpretations of aerial photographs.

Fir regeneration is often of very high density; for example, stocking levels of up to 148 000 stems·ha<sup>-1</sup> have been reported for young balsam fir stands (Moroni et al. 2005). Competition between dense regeneration suppressed diameter growth of individual trees in middle-aged unthinned harvested fir (F/H/M), producing high <9 cm DBH live tree C (Table 3). Balsam fir is thinned to promote the growth of residual trees and to reduce the age required for the production of merchantable diameter (≥9 cm DBH) trees. Precommercial thinning did generate more ≥9 cm DBH tree C ( $p < 0.1$ ) in middle-aged thinned harvested fir (F/HT/M) than in unharvested fir (F/H/M); however, total live tree C in the thinned strata ranked below (21% less) live tree C in the unthinned strata (Table 3). This suggests that a management practice, such as thinning, to increase merchantable stemwood is not necessarily compatible with increasing C sequestered in total live biomass.

Hardwoods are common in Newfoundland fir and spruce forests. Harvesting and hemlock looper outbreaks do not target hardwoods, increasing the proportion of hardwoods in live biomass following disturbance (Table 3). Thus, live tree C in recently disturbed fir (F/I/Y and F/H/Y) contained large proportions of hardwood C, with high hardwood biomass persisting to middle age for unthinned fir (F/I/M and F/H/M). Middle-aged thinned harvested fir (F/HT/M) contained less hardwood biomass than middle-aged unthinned harvested fir (F/H/M) because thinning targets unmerchantable trees, including hardwoods.

### Dead wood

Dead wood (dead standing trees, WD, buried wood, and stumps) abundance was comparable with values reported in forests composed of similar-sized trees (Moroni 2006). Although harvested strata had low snag C, natural disturbances generated large amounts of snag C (Table 3). Few snags had collapsed in the first 2 years following natural disturbance, but almost all snags had fallen after 32–41 years (Table 3). Snag abundance increased from strata regrown 32–41 years following disturbance to 63- to 109-year-old strata, but snags remained a minor C pool.

Natural disturbances generated little WD during the first 2 years following disturbance (Table 3). In contrast, harvesting immediately generated large amounts of WD C, mainly in small-diameter debris (Moroni 2006). Almost all harvest slash had collapsed or decomposed 32–41 years following harvesting, but naturally disturbed strata had generated large

amounts of WD C from the collapse of snags 32–41 years after disturbance (Table 3). Harvested strata contained less WD C 32–72 years following disturbance than strata disturbed naturally. Amounts of WD C in spruce strata regrown following harvesting and fire had converged 63–72 years following disturbance. Amounts of snags and WD in the 92-year-old spruce stratum regrown following fire (S/B/O) had begun to accumulate due to senescence (Moroni 2006). The C content of WD increased from strata regrown 32–72 years following disturbance to old growth aged 86–109 years. The impact of precommercial thinning on WD C was minor (Table 3) (Moroni 2006).

While buried wood formed a minor C pool, in some strata, equivalent amounts of C were found in buried dead wood and unburied dead wood (Table 3). Buried wood abundances were likely underestimated in this study. With organic horizons averaging 9–11 cm in thickness, it is possible that significant amounts of wood were buried below 2 cm and not recorded here; thus, buried wood could form a significantly larger C pool in Newfoundland boreal forests than was estimated here. Few studies record the presence of buried wood (Moroni 2006) and none, to our knowledge, have quantified it. Thus, buried wood and the processes through which it becomes buried are potentially significant to forest C budgets and warrant further study.

### Organic and mineral soil and total ecosystem C stocks

A large proportion of ecosystem C stocks in all strata was composed of mineral soil C and organic horizon C. Stocks were within the range reported in the literature for boreal species (e.g., Smith and Heath 2002; Ladegaard-Pedersen et al. 2005) but showed no trend with forest age or disturbance history in spruce (Table 3). Total ecosystem C stocks in spruce and fir showed no statistical trend with forest age or disturbance history (Table 3) because the inclusion of soil pools in the ecosystem total masked any trends observed in the live tree and dead wood C dynamics.

Studies show that harvesting decreased (Olsson et al. 1996), had no effect on (Peltoniemi et al. 2004), and increased the thickness and C content of the organic horizon (Mattson and Swank 1989). Increases are attributed to harvest slash (Mattson and Swank 1989) and decreases are attributed to the removal of harvest slash (Mahmood et al. 1999). Hence, recently harvested fir where slash was left on site was not expected to have low organic horizon C. Organic horizon C is expected to increase with forest age due to litterfall (Peltoniemi et al. 2004). Increases in organic horizon C with age were not observed under spruce in this study, but there is perhaps weak evidence for this under fir where F/U/O ranks above younger strata, except F/I/Y, for organic horizon C (Table 3). Others also reported no clear temporal patterns in organic horizon C following fire or harvesting and time since disturbance (e.g., Smith et al. 2000).

Soil C stocks are notoriously difficult to measure because of high spatial variability within and between plots or sites (Yanai et al. 2003; Conen et al. 2004). Within-site variability in soil C is often associated with factors that influence and are the result of pedogenesis (Shaw et al. 2008a). In this study, high spatial variability in the abundance of <2 mm soil and depth of soil development are likely important factors contributing to high variances estimated for

mean soil C values. A wide range in values for the proportion of coarse fragments (>2 mm diameter) in sampled soil was observed (data not shown) and during sampling, regions without significant mineral soil (organic horizon on rock) and mineral soils deeper than 45 cm were common.

High intersite variability for soil C may have prohibited detection of trends with time in this chronosequence study. The most striking example of site effects in this study can be seen when comparing older fir (F/U/O) and recently insect-killed fir (F/I/Y). Although, as expected, older fir (F/U/O) contained more mineral soil and organic horizon C than some younger strata (Table 3), recently insect-killed fir (F/I/Y) contained the largest organic horizon C stocks among strata and was the highest ranked stratum for mineral soil C stocks with almost double the mineral soil C of the second highest ranking stratum. Such large organic horizon and mineral soil C stocks in F/Y/I were not expected due to strata effects, where no large changes soil C stocks are expected in the 3 years following insect-induced mortality. Site effects are unknown, but we speculate that they involve soil pedogenic differences (Shaw et al. 2008a) and macro- and microtopographic and geographic features that influence soil temperature and drainage for at least periods of the annual cycle. These effects are further compounded by interactions with vegetation such as mosses (Oechel and Van Cleve 1986), which can also strongly influence litter cycles and forest floor C accumulation (Oechel and Van Cleve 1986; Harden et al. 1997).

Thus, it is not surprising that no significant trend in soil C could be detected with disturbance history or time since disturbance as reported in this study and others (e.g., Smith et al. 2000). Some of the challenges for detecting change in forest soil C may be overcome by developing more powerful sampling designs that consider within- and between-site characteristics influencing soil C stocks and stock changes (Yanai et al. 2003; Shaw et al. 2008b).

## Conclusions

Of the three largest forest C pools (mineral soil, organic horizon, and live tree), only live tree C changed predictably with disturbance history and time since disturbance, essentially increasing with forest age from lows immediately following stand-replacing disturbance. Site effects may have masked the ability to detect strata effects in mineral soil and organic horizon C dynamics. Tree growth appeared to be affected by disturbance history where regeneration under snags left following natural disturbance slowed growth compared with that of regeneration without residual snags. Snag shading contributes to variability in actual growth and yield, contributing to deviations from natural variability in forest development and the timing of senescence.

Snag and WD C stocks were temporally dynamic and strongly influenced by disturbance history and time since disturbance, but dead wood had a short lifespan and dead wood abundances in forests with different disturbance at origin converged at low levels 40–60 years following disturbance. Only in naturally disturbed strata was there significant accumulation of snags soon after disturbance. WD was relatively abundant in recently harvested and middle-aged naturally disturbed strata.

While thinning increased the biomass of merchantable

stems, thinned sites contained less total biomass C and did not maximize stand-level C.

Buried wood C stocks were relatively small but comparable with unburied downed dead wood stocks in some strata. Buried wood is a poorly understood forest C pool that requires further study.

The lack of trend in soil pools with time since disturbance emphasizes the need to increase the quantity and quality of forest soil C estimates using powerful sampling designs to enable detection of trends and changes.

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