Contrasting total carbon stocks between ecological site series in a subboreal spruce research forest in central British Columbia

Claudette H. Bois, Darren T. Janzen, Paul T. Sanborn, and Arthur L. Fredeen

Abstract: A study was conducted to determine if consideration of ecological site classification in combination with stand age would describe total ecosystem carbon (C) better than consideration of just stand age alone. The research was conducted in the 9250 ha University of Northern British Columbia/The University of British Columbia Aleza Lake Research Forest in central British Columbia. Over three field seasons (2003–2005), 38, 72, and 27 plots were established in mesic, subhygric, and hygric stands, respectively, with stand ages ranging from 5 to 350+ years. Mineral soil C stocks were significantly influenced by moisture regime, where hygric > subhygric > mesic (93, 77, and 65 t C·ha^{-1}, respectively). Mineral soil and forest floor C stocks were not related to stand age, indicating their resilience to partial-cut and clear-cut forest harvesting systems historically implemented throughout the study area. Subhygric stands had the highest total ecosystem C stocks in the Aleza Lake Research Forest, having approximately 18% more C than mesic and hygric stands, principally due to higher mineral soil C stocks (than mesic stands) and improved C sequestration in large trees (over hygric stands). Consideration of ecological site classification in addition to stand age information improved total ecosystem C stock estimates over the use of stand age alone.

Résumé : Cette étude a été réalisée dans le but de déterminer si la classification écologique d'une station combinée à l'âge du peuplement permet d'obtenir une meilleure estimation de la quantité totale de carbone (C) dans l'écosystème que celle qu'on obtient en tenant compte seulement de l'âge du peuplement. L'étude a été réalisée dans la forêt expérimentale du lac Aleza (UNBC et UBC) qui couvre 9250 ha dans le centre de la Colombie-Britannique. Pendant trois saisons de terrain (2003–2005), respectivement 38, 72 et 27 placettes ont été établies dans des stations mésiques, subhygriques et hygriques où l'âge du peuplement variait de 5 à 350 ans et plus. Les stocks de C dans le sol minéral étaient significativement influencés par le régime hydrique et atteignaient respectivement 93, 77 et 65 t·ha^{-1} dans les stations hygriques, subhygriques et mésiques. Les stocks de C dans le sol minéral et la couverture morte n'étaient pas reliés à l'âge du peuplement, ce qui est un indice de leur résilience aux régimes de coupe partielle et de coupe à blanc implantés depuis longtemps partout dans l'aire d'étude. Dans les stations subhygriques, on a observé les stocks de C total dans l'écosystème les plus élevés dans la forêt expérimentale, soit approximativement 18 % plus de C que dans les stations mésiques et hygriques, principalement à cause des stocks de C plus élevés dans le sol minéral, comparativement aux stations mésiques, et d'une meilleure séquestration du C chez les gros arbres, comparativement aux stations hygriques. Le fait de tenir compte de la classification écologique de la station, en plus de l'âge du peuplement, améliore les estimations du stock de C total dans l'écosystème comparativement à l'utilisation de seulement l'âge du peuplement.

[Traduit par la Rédaction]

Introduction

Carbon (C) stocks and sequestration in terrestrial ecosystems have garnered increased interest since the fourth Intergovernmental Panel on Climate Change Assessment (IPCC 2007) which has heightened climate change concerns, and with the Kyoto Protocol having entered its first reporting period (2008–2012). Under the Kyoto Protocol, participating countries are required to account for land-use change activities involving the conversion of forested land to nonforested land (deforestation), or nonforested land to forested land (reforestation or afforestation) (United Nations Framework Convention on Climate Change. Conference of the Parties (UNFCCC COP) 2002). In addition to C budgeting for land-use change, the Kyoto Protocol allows the inclusion of managed forest lands in National C budgets. As operational forest management is conducted at local scales, data detailing C dynamics at those same scales are required to allow effective C management and accounting (Kurz et al. 2002). For these reasons, an improved understanding of C stocks and sequestration in both natural and managed forests is required. The direct assessment of C stored in forest ecosystem stocks during stand development, the role that stand

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characteristics play in affecting these stocks, and the effects of operational forest management on C stocks would contribute to improved understanding for forest C management.

Total ecosystem carbon (TEC) reflects the summation of C stored in all component parts of a forest stand from soil organic matter to vegetation (Malhi et al. 1999; Bhatti et al. 2002; Smithwick et al. 2002). TEC is generally estimated using a combination of empirical and (or) simulation models based on forest cover, land-use, and soils information (Smith et al. 2004); few assessments of TEC are based on actual field observation and C stock measurements because of the time and money required to make them, particularly for large areas. Forest C estimates based on generalized vegetation classifications provide approximate estimates of C stocks in broad forest regions while omitting spatial heterogeneity common in forested landscapes (Smith et al. 2004). Remote sensing methodologies can be employed to describe C stocks or biomass spatially across a landbase (Mickler et al. 2002), but these types of studies also require plot data at the same spatial scale as the remote sensing data. At the same time, many forest C inventories fail to provide adequate assessments of belowground C stocks or understory vegetation, since the primary focus is typically on merchantable timber (Malhi et al. 1999), and non-canopy stocks are not accessible by standard remote sensing methods. Although some comprehensive field-based C stock assessment studies have been conducted (Lee et al. 2002; Smithwick et al. 2002), most have typically focussed on particular C stocks, and therefore, do not provide a viable estimate of TEC. Comprehensive C stock assessments are needed if we are to accurately determine the way in which forest management affects forest TEC and, thereby, improve C budget models. Additionally, by considering ecosystem complexity and the role of site characteristics in controlling C storage, the accuracy of TEC estimates may be improved for heterogeneous forested landscapes.

Large trees and soil organic matter represent the dominant aboveground and belowground contributors to TEC in temperate, tropical, and boreal forests, with the ratios of soil organic matter C to large tree (including roots) C averaging 37%, 44%, and 87%, respectively (Malhi et al. 1999). The high spatial variability of forest floor and woody debris C stocks presents an additional dimension of uncertainty in TEC assessments (Smith et al. 2000). In terms of quantifying TEC, it is generally believed that the knowledge regarding mineral soil, forest floor, and woody debris C stocks is deficient in terms of base-line information and the effects of forest management on their respective C stock dynamics (Hoover et al. 2000; Kurz et al. 2002). The dynamics of woody shrub C storage in savannas, deserts, and grasslands have been the focus of past studies (Jackson et al. 2002); however, little is known regarding woody shrub contribution to C storage in forested biomes. Although understory vegetation components are considered to be relatively minor C stocks in mature stands (Smith et al. 2004), assessments in natural and managed forest stands would enhance our understanding of their relative importance in different ages of managed and unmanaged stands.

Old-growth forests are known to contain higher amounts of C than that of earlier successional stages (following harvesting) of the same forest type principally because of large-tree C stocks (Smithwick et al. 2002; Fredeen et al. 2005). Component C stocks measured in old-growth forests may provide benchmarks from which to assess the impacts of forest management activities. Although past studies have assessed the impacts of clearcutting on forest C stocks (e.g., Jiang et al. 2002), the impacts of other forest management activities, such as thinning and shelterwoods have received little attention (Hoover et al. 2000). Comparatively, research describing soil and forest floor C stocks exists largely for clearcuts but is otherwise limited (Hoover et al. 2000). Further, the remaining understory vegetation stocks are infrequently measured following forest management (Smith et al. 2004). Knowledge is required not only of the immediate impact of forest management activities but also the subsequent recovery and (or) response over time for these C stocks. To balance C management with other objectives, such as biodiversity and timber production, forest managers need detailed knowledge of forest management impacts on C stocks and sequestration.

Dominant tree species, composition, and stand age are frequently and justifiably primary factors in determining C stocks and sequestration across forested landscapes (Kurz et al. 2002). For instance, it has been shown that the specific species that colonize disturbed sites will influence forest floor C sequestration (Ste. Marie et al. 2007). However, it is microsite characteristics, such as stand level soil texture, moisture, and nutrient availability, that influence tree growth, understory composition, and forest TEC (Bhatti et al. 2002). The resulting forest ecological site series may respond uniquely in terms of their C storage capacity in natural, managed, and recovering conditions. Previously, microsite characteristics were rarely described in forest inventory data sets and were, therefore, difficult to include in C budgets. In some jurisdictions, however, improvements in spatial forest cover data sets are in progress to describe microsite characteristics at the same scale at which forest inventory data are acquired (Grossman et al. 1998). A comprehensive understanding of C stocks and their relationships subject to different microsites will provide more ecologically sound forest C budgets (Banfield et al. 2002) and may facilitate better forest C management.

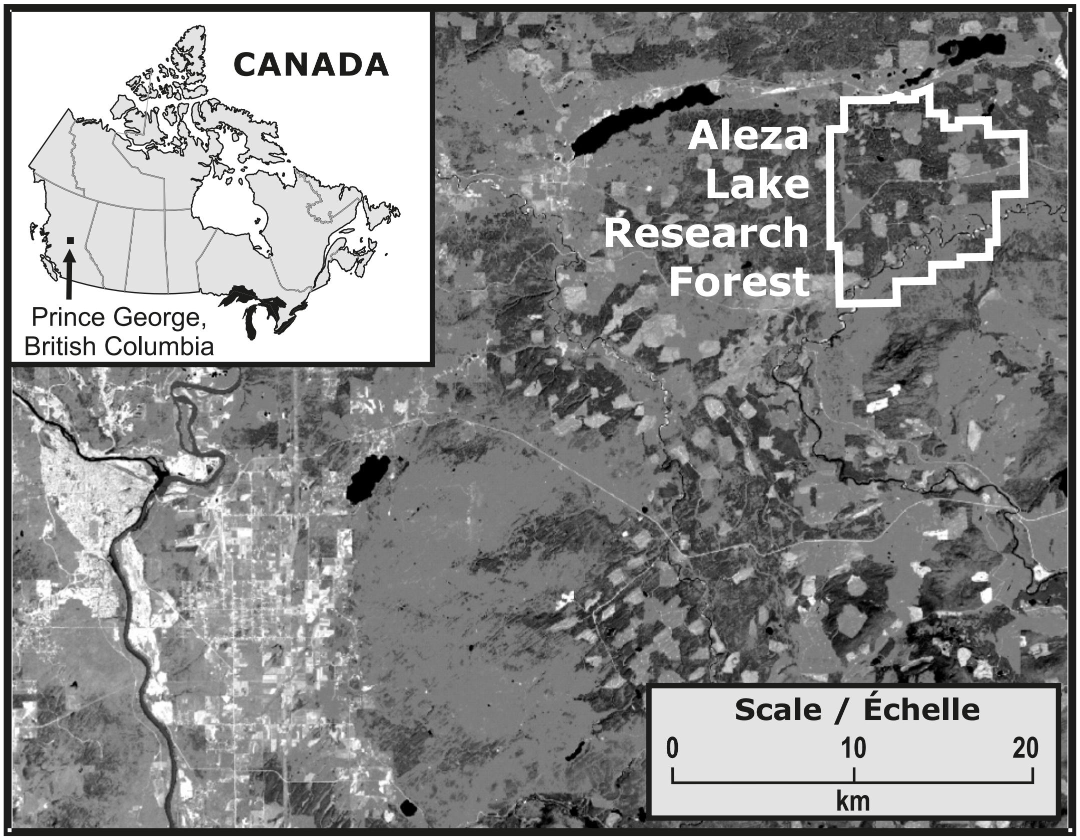
The principal questions addressed in this research were threefold: (1) What are the TEC and component C stocks for subboreal spruce and fir stands of differing ages? (2) What are the effects of local ecological site characteristics on C stocks? (3) How do total and component C stocks recover following forest harvest?

Methods and materials

Study area

A 3 year field-based comprehensive C stock assessment project was conducted from 2003 to 2005 in the 9250 ha University of Northern British Columbia – University of British Columbia Aleza Lake Research Forest (ALRF), located approximately 60 km east of Prince George in central British Columbia (54°03′11″N, 122°03′40″W; Fig. 1). The ALRF lies within the Sub-Boreal Spruce (SBS) biogeoclimatic zone and experiences a mean annual precipitation and temperature of 930 mm and 3.1 °C, respectively, thereby further classifying its subzone as both wet and cool

Fig. 1. Map of the Aleza Lake Research Forest near Prince George, British Columbia, Canada.



(SBSwk1; DeLong 2003). The topography of the ALRF is undulating, with elevation ranging from 600 to 750 m a.s.l. and with mesic, upland forests occurring in the northern region and hygric forests increasing towards the southern region in the vicinity of the Bowron river floodplain (Jull and Karjala 2005). Forest stands in the ALRF are dominated by subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and hybrid white spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.), with a few scattered Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and paper birch (*Betula papyrifera* Marsh.), as well as several species of *Populus*. Forest management at the ALRF has included various partial-cut and clear-cut silvicultural systems, typically followed in the latter by site preparation, including broadcast burning and (or) mechanical scarification. Partial cutting was generally diameter-limit horse logging conducted between 1940 and 1960. These operations typically removed 10%–30% of standing volume at that time (Jull and Karjala 2005). Clear-cutting has been the dominant timber harvesting regime since the 1960s, with hybrid white spruce and lesser amounts of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) as the predominant species replanted (Jull and Karjala 2005). Since no stand-replacing natural disturbance event has occurred in the ALRF over several hundred years, old-growth forests presently occupy approximately 39% of the research forest area.

Fine-textured glaciolacustrine deposits are the parent materials of the Luvisolic soils (Arocena and Sanborn 1999), which occupy approximately 80% of the ALRF. Gleyed Gray Luvisols and Luvic Gleysols dominate poorly drained regions and are characterized by organic matter accumulation in the A horizon, a blocky and impermeable Bt horizon, and a rooting depth limited to the forest floor and A horizons (Jull and Karjala 2005). Humo-Ferric Podzols found on coarse-textured glaciolacustrine and glaciofluvial sediments occupy better-drained sites and are characterized by an eluvial A horizon and Bf horizon overlying a heavily gleyed Bt horizon into which the rooting zone is extended (Jull and Karjala 2005).

The SBSwk1/01 ecological site series (DeLong 2003) represent mesic, upland forests commonly occurring on moderately sloping, silty clay to clay-textured soils (Table 1). Mesic stands are characterized by hybrid white spruce and subalpine fir, with a rich herb layer dominated by oak fern (*Gymnocarpium dryopterus*) and a dense moss layer (DeLong 2003). Mesic stands constitute approximately 18% of the ALRF; of these, 37% are old growth (175+ years old) while 22% are regenerating (0–20 years). The site index, defined as the mean height (m) of a typical unshaded tree at 50 years of age, and the mean gross volume of timber per hectare ($m^3 \cdot ha^{-1}$) of a typical old-growth mesic stand are 15.6 m and 368 $m^3 \cdot ha^{-1}$, respectively (Jull and Karjala 2005).

In the ALRF, subhygric forest stands commonly exist in complex mosaics of ecological site series SBSwk1/07 and SBSwk1/08. These subhygric stands occur on level or gently sloping, silty clay or clay-textured sites where a sand cap veneer overlies the clay-rich B horizon. Subhygric stands are characterized by hybrid white spruce and subalpine fir,

Table 1. Soil characteristics, area, dominance, and slope position of common ecological site series sampled for carbon at the Aleza Lake Research Forest in a subboreal spruce forest in British Columbia.

Ecological site series*	Area (ha)	Slope position†	Relative soil moisture regime*	Relative soil drainage regime†	Soil texture†
SBSwk1/01	1773	Upper	Mesic (18%)	Well drained	Silty clay loam to clay
SBSwk1/07 and SBSwk1/08	2561	Mid	Subhygric (26%)	Moderately to well drained	Sandy veneer over silty clay to clay
SBSwk1/09	1675	Lower	Hygric (17%)	Poorly drained	Silty clay to clay

*Adapted from DeLong 2003. Values in parentheses are the percentages of the moisture regime represented in the Aleza Lake Research Forest.
†Field observations.

by an understory dominated by black twinberry (*Lonicera involucrata*), devil's club (*Oplopanax horridus*), and oak fern (*Gymnocarpium dryopteris*), and by dense moss cover (DeLong 2003). Subhygric stands represent 26% of the ALRF, in which 41% and 21% are old-growth and regenerating stands, respectively. The site index for subhygric stands is 14.7 m and the mean volume of timber per hectare for a typical old-growth stand is 352 $m^3 \cdot ha^{-1}$ (Jull and Karjala 2005).

The SBSwk1/09 ecological site series are generally hygric, lowland forests occurring on level or depressional sites with fine-textured soils (DeLong 2003). These hygric stands are characterized by having a relatively sparse canopy of subalpine fir and hybrid white spruce with an understory dominated by horsetail (*Equisetum sylvaticum*) and moss (DeLong 2003). Hygric stands represent 17% of the ALRF, where 27% and 19% are old-growth and regenerating stands, respectively. The typical hygric stand has a site index of 13.6 m and a mean volume of timber per hectare of 303 $m^3 \cdot ha^{-1}$ in old-growth stands (Jull and Karjala 2005).

The three ecological site series described above were the focus of this research because of their area based dominance and forest management history in the ALRF. Because of their inherent differences in mineral soil moisture regimes, these ecological site series will be simply referred to as mesic (SBSwk1/01), subhygric (SBSwk1/07/08), and hygric (SBSwk1/09) for the duration of this paper.

Plot selection

Research plot locations were selected randomly within strata composed of the dominant ecological site series, stand ages, and management histories. In total, 137 plots were established over the summers of 2003 through 2005 — 38 mesic stands, 72 subhygric stands, and 37 hygric stands. Forest stands were grouped into four developmental stages: regenerating (0–20 years), juvenile (21–80 years), mature (81–174 years), and old growth (175+ years). The old-growth threshold of 175 years is based on stand age and structural complexity, as suggested by Kneeshaw and Burton (1998) and Wells et al. (1998) in the SBS. Plot tallies, broken down into regenerating, juvenile, mature, and old growth were, respectively, 12, 6, 7, and 13 in mesic stands; 13, 18, 21, and 20 in subhygric stands; and 9, 3, 8, and 7 in hygric stands.

Field-based C stock measurements

Data collection and sampling methodology were adapted from the National Forest Inventory Ground Sampling Guidelines of the Canadian Forest Service (Canadian Forest Inventory Committee 2002, version 1.1), as previously outlined in Fredeen et al. (2005). Briefly, the measurements were made as follows. Large trees (≥1.3 m tall and ≥9.0 cm in diameter at breast height (DBH)), both live and dead, were sampled nondestructively via measurement of DBH (1.3 m from the forest floor) by tree species over a 400 m^2 area around the plot center. Small trees, shrubs, and stumps (≥1.3 m in height and <9.0 cm in basal diameters) were similarly sampled but over a smaller area (50 m^2). Destructive sampling of woody shrubs (<1.3 m in height) and herbaceous plants and collection of fine woody debris (<1.0 cm in diameter) took place within four 1 m^2 microplots within the plot (Fredeen et al. 2005). Large (>7.5 cm diameter) woody debris was measured along two orthogonal 30 m transects by recording diameters, tilt angles, and decay classes (B.C. Ministry of Environment, Lands, and Parks and B.C. Ministry of Forests 1998). Small (1.0–7.5 cm diameter) woody debris was measured along these same transects with a tally system for three size ranges (1–3, 3–5, and 5–7.5 cm). Accumulations of piled downed wood were also measured along the two orthogonal 30 m transects by recording the width (cm), height (cm), length (cm), and percent density. Twelve independent volumetric forest floor samples were collected, three in each of the four microplots, using a fabricated coring bit (i.d. 5 cm) mounted on a battery-driven power drill (Nalder and Wein 1998). In plots established in 2004 and 2005, 12 independent additional forest floor samples were collected from four additional 1 m^2 microplots, as above. Two mineral soil pits were excavated, manually assessed for soil texture, moisture regime, drainage class, and horizon classifications (Soil Classification Working Group 1998; B.C. Ministry of Environment, Lands, and Parks and B.C. Ministry of Forests 1998), and subsampled using a 9.6 cm inside diameter steel cylinder and slide-hammer (Soilcon Laboratories, Richmond, British Columbia) in 6.6 cm increments to 47 or 107 cm in depth within two plot quadrats.

Biomass C estimates

Large-tree heights were estimated from recorded DBH values using allometric equations generated from ALRF permanent sampling plot data (C. Farnden and M. Jull, Prince George, British Columbia, unpublished data). Live large-tree volumes and aboveground biomass and biomass components of foliage, stem bark, stem wood, and branches were then estimated using the established allometric relationships of Penner et al. (1997), for volumes, and Standish et al. (1985), for biomasses, and where necessary *Alnus* and *Salix* species biomasses were estimated (Jenkins et al. 2003). To-

Table 2. Dead organic matter carbon stocks (tonnes C·ha^{-1}) in mineral soil, forest floor, total woody debris, and standing dead trees by ecological site series.

Ecological site series	No. of plots	Mineral soil 0–47 cm depth	Mineral soil 47–107 cm depth	Forest floor	Total woody debris*	Standing dead trees	Total DOM†
Mesic	38	65±3.3c	23±2.2a (*n* = 17)	28±1.9a	16±1.3a	0.27±0.07a	110±4.5b
Subhygric	72	77±2.3b	24±1.5a (*n* = 34)	38±3.4a	18±1.8a	0.38±0.08a	133±5.0a
Hygric	27	93±6.2a	25±5.8a (*n* = 9)	27±2.0a	15±1.4a	0.26±0.10a	135±6.5a

Note: Values are mean ± standard error. Means within a column sharing the same letter are not significantly different (Bonferroni, α = 0.05).
*Includes fine, small, and coarse debris.
†Dead organic matter (DOM) of the forest floor + mineral soil at 0–47 cm + woody debris + standing dead trees.

tal and fine-root biomasses were estimated using the allometric relationships of Li et al. (2003). Small-tree (2.5–9 cm DBH) total and component biomasses were estimated using the allometric relationships of Jenkins et al. (2003). Stem wood volumes of trees with DBH <2.5 cm were determined using small-tree (2.5–9 cm DBH) allometric relationships. Known wood densities for tree species in British Columbia were used for all small trees and shrubs (J. Parminter, Ministry of Forests, Victoria, British Columbia, unpublished data, 1997). National level allometric equations (Ung et al. 2008) were also available and produced plot-level results within 3% of the results obtained from the methods above. These methods were selected, as they were a better representation of the study area.

Large-tree C concentrations were taken from Lamlom and Savidge (2003). Shrub C contents were estimated using a measured number of stems, the mean stem dimensions, and the density of individual stems. C contents for fine woody debris, woody shrubs, and herbs were measured directly and as explained below. Coarse and small woody debris volumes were calculated using the line intersect method according to Van Wagner (1982) and Marshall et al. (2000). Small woody debris diameters used averages for each size range (1–3, 3–5, and 5–7.5 cm). Decay-class wood densities were used to convert woody debris volume to biomass (D. Sachs, Forest Research Ecologist, Kamloops, British Columbia, unpublished data, 1997). The C content of all woody debris, after correcting for density, was assumed to be 50% (Laiho and Prescott 1999).

Carbon content analysis

Forest floor and mineral soil samples were air-dried, their bulk densities determined, and then they were homogenized using a 2 mm sieve, a mortar and pestle, and a coffee grinder (Salton; model CG-7B). Fine woody debris, woody shrubs, and herbs were ground to a fine powder using a hammer mill (Micron Powder Systems, model W). The percentage of C was determined according to the Dumas-combustion method (Kirsten 1983), using an NA 1500 Elemental Analyzer (Fisons Instruments SP, Milano, Italy), where 18–22 mg of mineral samples or 4–8 mg of biomass samples were used. All samples were analyzed in duplicate, and total C concentration was interpreted as equivalent to organic C.

Statistical analyses

Simple linear regressions were performed on all component and total C stocks with stand age for mesic, subhygric, and hygric stands (Statistica 6.0, 2001). All C stock statistical analyses were performed on data expressed as mass of C per hectare. Total ecosystem and component C stocks were examined for single effects using one-way ANOVAs, while ecological site series, stand age, and their interaction effects were examined using two-way ANOVAs with PROC GLM procedures (SAS Institute Inc. 1989). All main effects were considered significant at α = 0.05. Means were compared using the Bonferroni test (α = 0.05; SAS Institute Inc. 1989).

Results

Stand origin

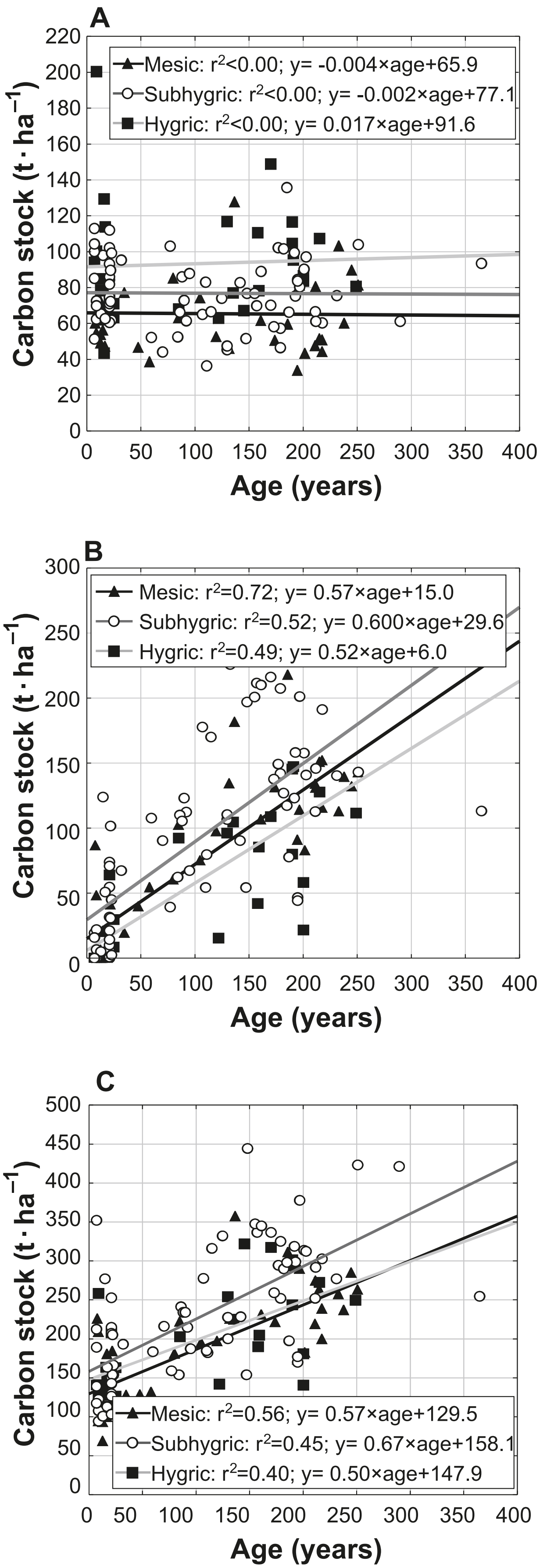
Some of the forested stands sampled in the research originated from 45- to 65-year-old partial-cut stands, as described previously. The ecosystem C stocks of these stands were compared with that of unharvested mature stands, and no significant differences were found for any pool. As such, these stands were included in the analyses using the age of the oldest tree within the stand, which always resulted in a mature (81–174 years old) classification of the stand.

Mineral soil, forest floor, standing dead trees, and woody debris C stocks

Mineral soil and forest floor C stocks did not differ significantly with stand age (shown for mineral soil, Fig. 2A). Therefore, data were lumped and a one-way ANOVA was used to determine the influence of ecological site series on mineral soil and forest floor C stocks (PROC GLM, SAS Institute Inc. 1989). Mineral soil C stocks were sampled at two depth increments, 0–47 and 47–107 cm. At the soil depth of 47–107 cm, the mineral soil C stocks ranged from 23 to 25 t C·ha^{-1} and were not significantly different among the ecological site series (Table 2). However, at the soil depth of 0–47 cm, mineral soil C stocks were significantly different among the ecological site series, with hygric stands (93 t C·ha^{-1}) having 21% and 42% more mineral soil C than subhygric (77 t C·ha^{-1}) and mesic (65 t C·ha^{-1}) stands, respectively (Bonferroni, α = 0.05; Table 2). Forest floor C stocks did not differ significantly among the ecological site series and ranged between 27 and 38 t C·ha^{-1} (Table 2).

Standing dead trees showed no significant differences by ecological site series or by stand age (Table 2). Woody debris C stocks in juvenile mesic and subhygric stands were significantly lower (58% and 63%, respectively) than those measured in old-growth stands of the same ecologi-

Fig. 2. Mineral soil (A), large tree (B), and total ecosystem (C) carbon stocks by age in three ecological site series (mesic, subhygric, and hygric), with trend lines from simple linear regressions. Mineral soil and total ecosystem carbon stocks were calculated based on mineral soil to 47 cm depth.



cal site series. By contrast, juvenile hygric woody debris C stocks were 68% higher (not significant) than those in old-growth hygric stands (Table 3). Juvenile-stand woody debris C stocks were significantly influenced by ecological site series, where hygric > subhygric > mesic (21.5, 10.7, and 8.0 t C·ha^{-1}, respectively), whereas old-growth subhygric woody debris C stocks significantly exceeded hygric woody debris C stocks by 55%. Regenerating and mature mesic, subhygric, and hygric stands had similar quantities of woody debris C.

Total belowground C stocks

Total belowground C stocks (defined here as mineral soil + forest floor + woody debris C stocks) measured in mesic, subhygric, and hygric stands did not vary with stand age (data not shown). Data were therefore grouped, and ecological site series' differences were evaluated using one-way ANOVAs. The results indicate that the total belowground C stocks in subhygric and hygric stands significantly exceeded the quantities measured in mesic stands by 20% and 23%, respectively (Table 2).

Total belowground C stocks measured in hygric stands consisted of 20% from the forest floor and 69% from the mineral soil (Table 2). By contrast, the total belowground C stocks measured in subhygric stands had both higher proportions from the forest floor (29%) and lower proportions from the mineral soil C (58%). Total belowground C stocks in mesic stands were intermediate, with 25% contributed from the forest floor and 59% from the mineral soil C. Woody debris C, averaged over all stand ages, comprised 11% of total belowground C stocks in hygric stands and 14% in both subhygric and mesic stands.

Herb, shrub, small-tree and total understory C stocks

In general, herb, shrub, small-tree and total understory C stocks did not differ significantly among ecological site series. Herb C stocks in regenerating stands were threefold that of mature and old-growth stands (Table 4). Similarly, shrub C stocks in regenerating stands were 1.5- to 2-fold that of juvenile, mature, and old-growth stands. In contrast, small-tree C stocks were highest in juvenile stands exceeding regenerating, mature, and old-growth stands by 61%. Total understory C stock trends resembled those for small trees, which contributed between 70% and 90% of the total understory C stocks, with the highest stocks in juvenile stands; the total understory C stock was 49% higher than the C stock of regenerating stands and 59% higher than that of both mature and old-growth forests. The percentage of total ecosystem C that is composed of herbs and shrubs was 0.8%, 0.6%, 0.2%, and 0.2% for regenerating, juvenile, mature, and old-growth stands, respectively. Similarly, the percentage of total biomass C that is composed of herbs and shrubs was 7.4%, 1.9%, 0.4%, and 0.4% for the same age groups.

Table 3. Total woody debris* carbon stocks (tonnes C·ha^{-1}) by age group for ecological site series.

Age group (years)	No. of plots	Mesic	Subhygric	Hygric
Regenerating (0–20)	34	15.8±2.2ab (*n* = 12)	15.4±3.8b (*n* = 13)	15.6±2.8a (*n* = 9)
Juvenile (21–80)	27	8.0±1.0b (*n* = 6)	10.7±1.6b (*n* = 18)	21.5±4.7a (*n* = 3)
Mature (81–174)	36	15.8±1.5ab (*n* = 7)	15.8±2.1b (*n* = 21)	13.8±2.4a (*n* = 8)
Old (175+)	40	18.9±2.6a (*n* = 13)	28.6±4.6a (*n* = 20)	12.8±2.4a (*n* = 7)

Note: Values are mean ± standard error. Means within a column sharing the same letter are not significantly different (Bonferroni, α = 0.05).

*Includes fine, small, and coarse debris. Fine woody debris is <1.0 cm diameter, small woody debris is 1 cm ≤ x ≤ 7.5 cm diameter, and coarse woody debris is >7.5 cm diameter (Canada Forest Inventory Committee 2002).

Table 4. Aboveground carbon stocks (tonnes C·ha^{-1}) of herb, shrub, small tree, total understory, large tree, total biomass, and total ecosystem by age.

Age group (years)	No. of plots	Herb*	Shrub*	Small tree†	Total understory‡	Large tree§	Total biomass‖	Total ecosystem¶
Regenerating (0–20)	34	0.36±0.04a	0.90±0.11a	2.8±0.8b	4.1±0.8b	13±5b	17±5c	148±10b
Juvenile (21–80)	27	0.30±0.13ab	0.62±0.11ab	7.1±1.5a	8.0±1.5a	40±6b	48±6b	164±7b
Mature (81–174)	36	0.12±0.02b	0.43±0.04b	2.7±0.5b	3.2±0.5b	123±9a	126±9a	248±12a
Old (175+)	40	0.12±0.05b	0.44±0.06b	2.8±0.4b	3.4±0.4b	130±8a	133±7a	268±10a

Note: Values are mean ± standard error. Means within a column sharing the same letter are not significantly different (Bonferroni, α = 0.05).

*Herb and shrub data do not include root C.

†Small trees include trees with a DBH <9.0 cm and a height >1.3 cm. The data include all biomass components (i.e., stemwood, stembark, branches, foliage, and roots) except for tree seedlings with a DBH <2.5 cm.

‡Total understory carbon constitutes that of herb + shrub + small tree.

§Large trees include those with a DBH ≥9.0 cm and a height >1.3 m. Large-tree C stocks include all biomass components (i.e., stemwood, stembark, branches, foliage, and roots). Large-tree C reflects live trees only.

‖Total biomass includes C from herb + shrub + small tree + large tree.

¶Total ecosystem biomass includes C from total biomass + total belowground (to 47 cm depth).

Large-tree and total biomass C stocks

Large-tree and total biomass C stocks did not differ significantly among ecological site series in any of the age groups, although similar trends in stand development were observed. As a result, ecological site series were pooled and one-way ANOVAs were used to determine significant age-group effects on large-tree and total biomass C stocks. As expected, clear-cut harvesting significantly reduced large-tree and total biomass C stocks to approximately 10% and 13%, respectively, of that of old-growth levels, on average, between 0 and 20 years after harvesting (Table 4; Fig. 2B). Large-tree and total biomass C stocks in 20- to 80-year-old stands continued to be significantly lower measuring 31% and 36% of old-growth stands, respectively.

A strong positive correlation between stand age and large-tree C was indicated by high r^2 values of linear regression against stand age (Fig. 2B). The large-tree and live biomass demonstrate the reduced rate of C sequestration in older stands, with increases of only 8% in both large-tree and live biomass C stocks from mature stands to old stands. Large-tree C accounted for 76% of total biomass C in regenerating stands (0 to 20 years of age) and 97% in old-growth stands. By contrast, the percentage of total biomass C in understory C decreased from 24% in regenerating stands to only 3% in old-growth stands.

Total ecosystem C stocks

Although mesic, subhygric, and hygric stands differed significantly in both mineral soil and total belowground C stocks, no ecological site series differences were observed in total ecosystem C, principally because of the lack of a significant effect of ecological site series on aboveground C stocks. Similar to large-tree and total biomass C stocks, total ecosystem C stocks in regenerating and juvenile stands were approximately 40% lower than that in mature and old-growth levels (Table 4).

A consistently strong relationship between stand age and total ecosystem C was observed in mesic, subhygric, and hygric stands. Not surprising is that the average annual C sequestration rate was similar in magnitude to that found in large-tree C stocks, indicating that the annual C sequestration rate was highly dependent on this stock (Fig. 2C). Although subhygric stands have both the largest initial C stock (at age zero) and the largest average annual C sequestration rate, the large variance observed in these stocks resulted in no overall significance being found for TEC among ecological site series. The ratio of live biomass to dead organic matter C found in regenerating stands was 1:8 and decreased to 1:2.5 in juvenile stands and 1:1 in mature and old-growth stands.

Discussion

Mineral soil and forest floor C stocks are often believed to experience reductions following clear-cut harvesting because of the increased rates of decomposition and reduced inputs of forest litter (Pennock and van Kessel 1997). Nevertheless, some research has shown only minor changes in soil C (Johnson 1992) following forest harvest. In the present study, linear regressions of mineral soil and forest floor C stocks by age revealed r^2 values that were ≤0.01 (shown for mineral soil; Fig. 2A), indicating that stand age had no effect on mineral soil and forest floor C stocks. These trends are in agreement with our initial findings that contrasted C stocks between soil types (Fredeen et al. 2005). However, the chronosequence approach used in this study would require a large change to reliably detect a significant effect (Yanai et al. 2003). Given the variability in forest floor and mineral soil in mature subhygric stands, regenerating subhygric stands would have needed to be 25.6% and 33.5% smaller (assuming the same variability) to detect a significant difference for mineral soil and forest floor C, respectively. Smith (2004) illustrates that if an event occurred that increased C inputs into a soil by 100% indefinitely, it would take 21 years to detect a 25% difference in the soil C.

Significant differences were observed in mineral soil C stocks as a function of ecological site series (Table 2). In the ALRF, the average mineral soil C stocks for mesic, subhygric, and hygric sites were 65, 77, and 93 t·ha^{-1} to 47 cm in depth and 88, 101, 118 t·ha^{-1} to 107 cm in depth, respectively (Table 2). These values are similar to that of mineral soil C stocks found in boreal forests of Alberta, Saskatchewan, and Manitoba (102, 82, and 107 t·ha^{-1} to 1 m, respectively; Tarnocai and Lacelle 1996), but they are lower than that found in the boreal forests of Ontario (138 t·ha^{-1} to 1 m; Lee et al. 2002) and in coastal old-growth and montane forests in Washington and Oregon (365 and 195 t·ha^{-1} to 1 m, respectively; Smithwick et al. 2002).

For mesic and hygric sites, the variance in forest floor measurements was highest in regenerating stands. By contrast, forest floor C stocks in subhygric stands revealed high variances at every stand age. Overall, the mean forest floor C stocks ranged from 27 to 38 t·ha^{-1}, which is consistent with that found in boreal forests of Alberta, Saskatchewan, and Manitoba (24, 34, and 21 t·ha^{-1}; Bhatti et al. 2002) but is somewhat higher than that in the old-growth coastal and montane forests of Washington and Oregon (12–22 t·ha^{-1}; Smithwick et al. 2002).

Woody debris C stocks were found to have significant differences among age groups and among ecological site series. Mesic and subhygric stands exhibited the expected 'u'-shaped pattern (Spies et al. 1988), whereas hygric stands did not, presumably because only three plots resided within the juvenile age class for this ecological site series. By averaging the results for mesic and subhygric plots, the mean woody debris C stocks, broken down by age group, were 15.6, 10.0, 15.8, and 24.8 t·ha^{-1} for regenerating, juvenile, mature, and old-growth stands, respectively. For comparison with other published results, these woody debris C stocks were converted to volumes, resulting in 171, 121, 181, and 257 m^3·ha^{-1} for the same age groups. This range of woody debris C stocks is substantially higher than that reported in a study within the same biogeoclimatic zone in British Columbia (SBSwk: 21–101 m^3·ha^{-1}; Feller 2003) but is within the range reported for an adjacent zone, which tends to receive moderately less precipitation (SBSmk: 41–532 m^3·ha^{-1}; Densmore et al. 2004). Boreal forests in Newfoundland showed the same trend with stand age but had lower C stocks for each period (68, 17, and 48 m^3·ha^{-1} in young, regenerating, and mature stands, respectively; Sturtevant et al. 1997), whereas forests in the cascade range of western Oregon and Washington had the same trend but with roughly twice the C stocks (46, 25, and 86 t·ha^{-1} in young, regenerating, and mature stands respectively; Spies and Franklin 1988).

In boreal forests in Ontario, herb and shrub components make up approximately 1% of the total biomass in mature forests (Lee et al. 2002), which is roughly twice that found in the ALRF. Smithwick et al. (2002) note that in coastal old-growth and montane forests, an increase of 10 000% in shrub biomass would increase the total ecosystem C by only 10%. The same percentage increase in the ALRF would increase the total ecosystem C by 21%, but the diminutive nature of these stocks are consistent with the conclusions of Smithwick et al. (2002). Thus, despite the large relative variation in the total stocks present in these two ecosystem components, their minimal contribution to the total ecosystem C may warrant their exclusion from C-accounting exercises in forests similar to this study area. However, if other forest values were to be examined (e.g., biodiversity and ecosystem function), their relative importance would greatly exceed their C stocks contributions.

Small- and large-tree C stocks were not significantly affected by ecological site series. For obvious reasons (i.e., forest succession and development), small-tree C stocks were at least 250% greater in juvenile stands than in stands of the other age groups. Not surprising, large-tree C stocks were found to increase with stand age, where the increase from regenerating stands to old-growth stands was 10-fold. Large-tree C stocks were the only components that showed a consistently strong positive relationship with stand age, where r^2 values ranged from 0.52 to 0.72 (Fig. 2B). In old-growth stands, small- and large-tree C stocks were 2.8 and 130 t·ha^{-1}, respectively. These measurements are substantially higher than those in boreal forests, ranging from a low of 19 t·ha^{-1} (Botkin and Simpson 1990) to a high of 69 t·ha^{-1} (Houghton et al. 1983), but are significantly lower than those in old-growth coastal and montane forests in western Oregon and Washington (364–465 t·ha^{-1}; Smithwick et al. 2002).

The live biomass C to dead organic matter C ratio ((large tree (including roots) + small tree + shrub + herb) : (mineral soil + forest floor + woody debris + standing dead wood)) ranged from ~1:8 in regenerating stands to ~1:1 in mature and old-growth stands. Old-growth ratios were similar to those found for tropical forests (~1:0.7), higher than temperate forests (~1:0.3), and considerably lower than levels recorded for northern boreal stands of central Canada (~1:6.9; Malhi et al. 1999). Total belowground C stocks were approximately equal in regenerating and old-growth stands and were moderately lower in both juvenile and mature stands, although none of these differences were significant. Total belowground C stocks in mesic stands were significantly lower than those in subhygric and hygric stands, due almost entirely to lower soil C stocks. Overall, belowground C stocks appear to be relatively resilient to the types of forest management that have been conducted at the ALRF, e.g., partial- and clear-cut harvesting of primary forest, with harvesting chiefly conducted in the winter on frozen ground.

Total biomass C stocks were not significantly different as a function of ecological site series but did show strong relationships with stand age. This was due primarily to the growth of the large-tree pool, which dominates total aboveground biomass. The same was true of total ecosystem C as indicated by the similarity in the slopes of the linear regression analyses conducted on large trees, biomass, and total ecosystem C. In this study, subhygric stands were found to have the highest initial total ecosystem C stock and the highest C sequestration rate (158 $t \cdot ha^{-1}$ and 0.67 $t \cdot ha^{-1} \cdot year^{-1}$, respectively; Fig. 2C). Mesic stands had the lowest initial C stock but the median C sequestration rate (130 $t \cdot ha^{-1}$ and 0.57 $t \cdot ha^{-1} \cdot year^{-1}$, respectively; Fig. 2C), while hygric stands had the median C stock but lowest C sequestration rate (148 $t \cdot ha^{-1}$ and 0.50 $t \cdot ha^{-1} \cdot year^{-1}$, respectively; Fig. 2C). Although it should be noted that the range of plot ages used in the analysis can influence an inferred linear sequestration rate, the rates above are comparable, as they are similar stand age ranges. Mesic and hygric stands had total ecosystem C stocks similar to that in old-growth stands, as the increased C sequestration in large-tree biomass in mesic stands was compensated for by the higher belowground C stock accumulation in hygric stands.

The effect of ecological site series at the ALRF on ecosystem components was not significant for any aboveground ecosystem component. Although the difference between means of the ecological site series on aboveground ecosystem components was as much as 36% in mature stands (difference between hygric and subhygric mature stands for large-tree C stocks), no significant differences were found in any of the aboveground ecosystem components. Ecological site series effects were found to be significant for both mineral soil and total belowground C stocks, with maximum differences of 43% and 23%, respectively. In the ALRF, subhygric stands tended to have higher total ecosystem C stocks than mesic and hygric stands, which were approximately equal in mature stands. Other research involving biomass or C stocks as a function of ecological site series is relatively rare. In a study of whole-tree biomass in lodgepole pine stands in south-eastern British Columbia, it was found that mesic stands contained over twice as much biomass per hectare as xeric stands (xeric, 158 $t \cdot ha^{-1}$; mesic, 330 $t \cdot ha^{-1}$; Comeau and Kimmins 1989). Reduced aboveground biomass in poorly drained sites relative to well-drained sites was reported for spruce–fir forests in Maine (Williams et al. 1991).

Forest C accounting activities generally consider the size of C pools and the rates of change over time in those pools. In this study, stand age can be considered to be a proxy for time, in which case, the rate of change over time is most significantly affected by continuous gains in large-tree C. Continuous gains were not observed in small-tree, herb, or woody debris C stocks, where some temporal periods exhibited stagnancy or losses of C. Forest floor and mineral soil did not exhibit any significant rate of change over time, indicating that for this study area, they may not need to be explicitly considered when accounting for forest management activity impacts on C sequestration. For the purposes of calculating the size of C pools, both stand age and ecological site series would need to be considered, as most aboveground C pools were significantly impacted by stand age, while belowground C pools were significantly affected by ecological site series. Determining the size of forest C pools is important for determining the impacts of land-use change, such as conversion from forested land to developed land. Our research indicates that the magnitude of the C footprint related to the conversion from forest land to developed land should explicitly consider the ecological site series and the stand ages of the area. With increasing forest soil moisture, biomass C increases to a point but is ultimately impeded by poor drainage in the wettest sites (i.e., hygric). By contrast, soil C stocks increase along the full gradient of increasing forest moisture with highest stocks in poorly drained hygric sites.

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References

Arocena, J.M., and Sanborn, S. 1999. Mineralogy and genesis of selected soils and their implications for forest management in central and northeastern British Columbia. Can. J. Soil Sci. **79**: 571–592.

Banfield, G.E., Bhatti, J.S., Jiang, H., and Apps, M.J. 2002. Variability in regional scale estimates of carbon stocks in boreal forest ecosystems: results from west-central Alberta. For. Ecol. Manage. **169**: 15–27. doi:10.1016/S0378-1127(02)00292-X.

B.C. Ministry of Environment Land and Parks and B.C. Ministry of Forests. 1998. Field manual for describing terrestrial ecosystems. Land Manage. Handb. 25.

B.C. Ministry of Forests. 1992. An old-growth strategy for British Columbia. B.C. Ministry of Forests, Victoria, Canada.

Bhatti, J.S., Apps, M.J., and Tarnocai, C. 2002. Estimates of soil organic carbon stocks in central Canada using three different approaches. Can. J. For. Res. **32**: 805–812. doi:10.1139/x01-122.

Botkin, D.B., and Simpson, L.G. 1990. Biomass of the North American boreal forest. Biogeochemistry, **9**: 161–174.

Canadian Forest Inventory Committee. 2002. National forest inventory ground sampling guidelines, version 1.1 [online]. Available from http://nfi.cfs.nrcan.gc.ca/index_e.html [accessed 20 February 2008].

Comeau, P.G., and Kimmins, J.P. 1989. Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. Can. J. For. Res. **19**(4): 447–454. doi:10.1139/x89-070.

DeLong, C. 2003. A field guide to site identification and interpretation for the southeast portion of the Prince George forest region. Land Manage. Handbook. No. 51. B.C. Ministry of Forests, Victoria, B.C.

Densmore, N., Parminter, J., and Stevens, V. 2004. Coarse woody debris: inventory, decay modelling, and management implications in three biogeoclimatic zones. B.C. J. Ecosyst. Manag. **5**: 14–29.

Feller, M.C. 2003. Coarse woody debris in the old-growth forests of British Columbia. Environ. Rev. **11**: S135–S157. doi:10.1139/a03-008.

Fredeen, A.L., Bois, C.H., Janzen, D.T., and Sanborn, P.T. 2005. Comparison of coniferous forest carbon stocks between old-growth and young second-growth forests on two soil types in central British Columbia, Canada. Can. J. For. Res. **35**: 1411–1421. doi:10.1139/x05-074.

Grossman, D.H., Faber-Langendoen, D., Weakley, A.S., Anderson, M., Bourgeron, P., Crawford, R., Goodin, K., Landaal, S., Metzler, K., Patterson, K., Pyne, M., Reid, M., and Sneddon, L. 1998. Terrestrial vegetation of the United States volume 1: the national vegetation classification system: development, status, and applications. The Nature Conservancy. Available from http://www.natureserve.org/library/vol1.pdf [accessed 20 February 2008].

Hoover, C.M., Birdsey, R.A., Heath, L.S., and Stout, S.L. 2000. How to estimate carbon sequestration on small forest tracts. J. For. **98**: 13–17.

Houghton, R.A., Hobbie, J.E., Melillo, J.M., Moore, B., Peterson, B.J., Shaver, G.R., and Woodwell, G.M. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980; a net release of CO_2 to the atmosphere. Ecol. Monogr. **53**: 235–262. doi:10.2307/1942531.

Intergovernmental Panel on Climate Change. 2007. Climate change 2007: synthesis report [online]. Available from http://www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf [accessed 20 February 2008].

Jackson, R.B., Banner, J.L., Jobbagy, E.G., Pockman, W.T., and Wall, D.H. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature, **418**: 623–626. doi:10.1038/nature00910. PMID:12167839.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., and Birdsey, R.A. 2003. National-scale biomass estimators for United States tree species. For. Sci. **49**(1): 12–35.

Jiang, H., Apps, M.J., Peng, C., Zhang, Y., and Liu, J. 2002. Modelling the influence of harvesting on Chinese boreal forest carbon dynamics. For. Ecol. Manage. **169**: 65–82. doi:10.1016/S0378-1127(02)00299-2.

Johnson, D. 1992. Effects of forest management on soil carbon stores. Water Air Soil Pollut. **64**: 83–120. doi:10.1007/BF00477097.

Jull, M., and Karjala, M. 2005. Aleza Lake Research Forest: management plan #2. British Columbia Ministry of Forests, Prince George Forest District.

Kirsten, W. 1983. Organic elemental analysis: ultramicro, micro and trace methods. Academic Press/Harcourt Brace Jovanovich, New York, USA.

Kneeshaw, D.D., and Burton, P.G. 1998. Assessment of functional old-growth status: a case study in the sub-boreal spruce zone of British Columbia, Canada. Nat. Areas J. **18**: 293–308.

Kurz, W.A., Apps, M., Banfield, E., and Stinson, G. 2002. Forest carbon accounting at the operational scale. For. Chron. **78**: 672–679.

Laiho, R., and Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. Can. J. For. Res. **29**: 1592–1603. doi:10.1139/cjfr-29-10-1592.

Lamlom, S.H., and Savidge, R.A. 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenergy, **25**: 381–388. doi:10.1016/S0961-9534(03)00033-3.

Lee, J., Morrison, I.K., Leblanc, J.-D., Dumas, M.T., and Cameron, D.A. 2002. Carbon sequestration in trees and regrowth vegetation as affected by clearcut and partial cut harvesting in a second-growth boreal mixedwood. For. Ecol. Manage. **169**: 83–101. doi:10.1016/S0378-1127(02)00300-6.

Li, Z., Kurz, W.A., Apps, M.J., and Beukema, S.J. 2003. Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. Can. J. For. Res. **33**(1): 126–136. doi:10.1139/x02-165.

Malhi, Y., Baldocchi, D.D., and Jarvis, P.G. 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. **22**: 715–740. doi:10.1046/j.1365-3040.1999.00453.x.

Marshall, P.L., Davis, G., and LeMay, V.M. 2000. Using line intersect sampling for coarse woody debris. Tech. Rep. TR-003, Research Section, Vancouver Forest Region, British Columbia Ministry of Forests.

Mickler, R.A., Earnhardt, T.S., and Moore, J.A. 2002. Regional estimation of current and future forest biomass. Environ. Pollut. **116**: S7–S16. doi:10.1016/S0269-7491(01)00241-X. PMID:11833920.

Nalder, I.A., and Wein, R.W. 1998. A new forest floor corer for rapid sampling, minimal disturbance and adequate precision. Silva Fenn. **32**(4): 373–382.

Penner, M., Power, K., Muhairwe, C., Tellier, R., and Wang, Y. 1997. Canada's forest biomass resources: deriving estimates from Canada's forest inventory. Inf. Rep. BC-X-370, Pacific Forestry Centre, Victoria, B.C., Canada. p. 33.

Pennock, D.J., and van Kessel, C. 1997. Effect of agriculture and clear-cut forest harvest on landscape-scale soil organic carbon storage in Saskatchewan. Can. J. Soil Sci. **77**: 211–218.

SAS Institute Inc. 1989. SAS/STAT user's guide. Version 6. Fourth edition. SAS Institute Inc., Cary, N.C., USA.

Smith, P. 2004. How long before a change in soil organic carbon can be detected? Glob. Change Biol. **10**: 1878–1883. doi:10.1111/j.1365-2486.2004.00854.x.

Smith, C.K., Coyea, M.R., and Munson, A.D. 2000. Soil carbon, nitrogen, and phosphorus stocks and dynamics under disturbed black spruce forests. Ecol. Appl. **10**: 775–788. doi:10.1890/1051-0761(2000)010[0775:SCNAPS]2.0.CO;2.

Smith, J.E., Heath, L.S., and Woodbury, P.B. 2004. How to estimate forest carbon for large areas from inventory data. J. For. **102**: 25–31.

Smithwick, E.A.H., Harmon, M.E., Remillard, S.M., Acker, S.A., and Franklin, J.F. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecol. Appl **12**(5): 1303–1317. doi:10.1890/1051-0761(2002)012[1303:PUBOCS]2.0.CO;2.

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd ed. Agriculture and Agri-Food Canada. Publ. No. 1646.

Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology, **69**: 1689–1702. doi:10.2307/1941147.

Standish, J.T., Manning, G.H., and Demaerschalk, J.P. 1985. Development of biomass equations for British Columbia tree species. Canadian Forest Service, Victoria, B.C., Inf. Rep. BC-X-264.

Ste. Marie, C., Pare, D., and Gagnon, D. 2007. The contrasting effects of aspen and jack pine on soil nutritional properties depend on parent material. Ecosystems, **10**: 1299–1310.

Sturtevant, B.R., Bissonette, J.A., Long, J.M., and Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol. Appl. **7**: 702–712. doi:10.1890/1051-0761(1997)007[0702:CWDAAF]2.0.CO;2.

Tarnocai, C., and Lacelle, B. 1996. Soil organic carbon of Canada data base (digital data base). Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Research Branch, Ottawa, Ont., Canada.

Ung, C.-H., Bernier, P., and Guo, X.-J. 2008. Canadian national biomass equations: new parameter estimates that include British

Columbia data. Can. J. For. Res. **38**: 1123–1132. doi:10.1139/X07-224.

United Nations Framework Convention on Climate Change. Conference of the Parties (UNFCCC COP) 2002. Report of the Conference of the Parties on its seventh session, held at Marrakesh from 29 October to 10 November 2001, addendum, part two: Action taken by the Conference of the Parties, Volume I. FCCC/CP/2001/13/Add.1 [21 January 2002].

Van Wagner, C.E. 1982. Practical aspects of the line intersect method. Petawawa National Forestry Institute, Canadian Forest Service, Petawawa, Ont., Canada. Inf. Rep. PI-X-12.

Wells, R.W., Lertzman, K.P., and Saunders, S.C. 1998. Old-growth definitions for the forests of British Columbia, Canada. Nat. Areas J. **18**(4): 279–292.

Williams, R.A., Hoffman, B.F., and Seymour, R.S. 1991. Comparison of site index and biomass production of spruce–fir stands by soil drainage class in Maine. For. Ecol. Manage. **41**: 279–290. doi:10.1016/0378-1127(91)90109-9.

Yanai, R.D., Currie, W.S., and Goodale, C.L. 2003. Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. Ecosystems, **6**: 197–212. doi:10.1007/s10021-002-0206-5.