Comparison of coniferous forest carbon stocks between old-growth and young second-growth forests on two soil types in central British Columbia, Canada

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

Abstract: Carbon (C) stocks were assessed for hybrid interior spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.)-dominated upland forests within the Aleza Lake Research Forest in central British Columbia, Canada. Four old-growth (141–250 years old) and four young second-growth (<20 years old) forest plots were established on the two dominant soil texture types, coarse and fine, for a total of 16 plots. Mean total C stocks for old-growth stands ranged from 423 Mg C·ha^{-1} (coarse) to 324 Mg C·ha^{-1} (fine), intermediate between Pacific Northwest temperate forests and upland boreal forests. Total C was lower in second-growth stands because of lower tree (mostly large tree stem), forest floor, and woody debris C stocks. In contrast, old-growth forest-floor C stocks ranged from 78 Mg C·ha^{-1} (coarse) to 35 Mg C·ha^{-1} (fine), 2.9- and 1.2-fold higher than in corresponding second-growth stands, respectively. Woody debris C stocks in old-growth stands totaled 35 Mg C·ha^{-1} (coarse) and 31 Mg C·ha^{-1} (fine), 2.7- and 3.4-fold higher than in second-growth stands, respectively. Mineral soil C to 1.07 m depth was similar across soil type and age-class, with totals ranging from 115 to 106 Mg C·ha^{-1}. Harvesting of old-growth forests in sub-boreal British Columbia lowers total C stocks by 54%–41%.

Résumé : Les stocks de carbone (C) ont été évalués pour les forêts de montagne dominées par l'épinette hybride de l'intérieur (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.) dans les limites de la forêt expérimentale du lac Aleza située dans le centre de la Colombie-Britannique, au Canada. Des parcelles-échantillons ont été établies dans quatre vieilles forêts (141–250 ans) et quatre jeunes forêts de seconde venue (<20 ans) sur les deux types dominants de texture du sol, grossière et fine, pour un total de 16 parcelles-échantillons. Les stocks totaux moyens de C pour les vieilles forêts variaient de 423 Mg C·ha^{-1} (grossière) à 324 Mg C·ha^{-1} (fine), à mi-chemin entre les forêts tempérées du Pacifique Nord-Ouest et les forêts boréales de montagne. Le C total était plus faible dans les peuplements de seconde venue parce que les stocks de C étaient plus faibles dans les arbres (surtout des arbres avec de grosses tiges), la couverture morte et les débris ligneux. À l'inverse, les stocks de C dans la couverture morte des vieilles forêts variaient de 78 Mg C·ha^{-1} (grossière) à 35 Mg C·ha^{-1} (fine), soit respectivement 2,9 et 1,2 fois plus que dans les peuplements de seconde venue correspondants. Les stocks de C dans les débris ligneux des vieilles forêts totalisaient 35 Mg C·ha^{-1} (grossière) et 31 Mg C·ha^{-1} (fine), soit respectivement 2,7 et 3,4 fois plus que dans les peuplements de seconde venue. Le contenu en C du sol minéral, jusqu'à une profondeur de 1,07 m, était similaire pour tous les types de sol et toutes les classes d'âge avec des totaux variant de 115 à 106 Mg C·ha^{-1}. La récolte des vieilles forêts dans la zone sub-boréale en Colombie-Britannique réduit les stocks totaux de C de 54 % à 41 %.

[Traduit par la Rédaction]

Introduction

Forests represent tremendous reservoirs of carbon (C): over half the world's terrestrial organic soil and vegetation C (~1150 Pg) is currently resident in forests (Intergovernmental Panel on Climate Change (IPCC) 2000; Prentice et al. 2001), with one half of this in boreal forests alone. In the absence of human intervention and natural stand-destroying events, forest ecosystem C is in relative equilibrium with atmospheric CO_2-C over relevant temporal (e.g., century) and spatial (e.g., hectares to square kilometres) scales through a balance of photosynthetic C gains with decomposition and respiration C losses. However, the overall trend for global forests has been and continues to be one of net deforestation (i.e., conversion of forest to nonforest), most recently in tropical regions (IPCC 2000). Historically, deforestation has contributed to one-third of the total rise in CO_2 since 1850 and still explains 20% of the rise in recent decades (IPCC 2000). Rising CO_2 in the atmosphere (nearly 35% higher than in preindustrial times), along with lesser contributions from other greenhouse gases, is currently believed to be the primary cause of the current global warming trend (Prentice

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et al. 2001). Considerable uncertainty about the way in which elevated CO_2 (Karnosky 2002), climate change (Gates 1993), and interactions of these factors with other variables (Thornton et al. 2002; Prentice et al. 2001) will affect trees and forests limit our ability to predict the future of forest ecosystems and their C stocks.

Unlike tropical forests as a whole, harvesting of boreal forests is largely followed by replanting or natural reforestation (Prentice et al. 2001). Nevertheless, conversion of old boreal forests to young plantations or managed forests also generally contributes CO_2 to the atmosphere (Harmon et al. 1990; IPCC 2000; Schulze et al. 2000; Thornley and Cannell 2000), although the magnitude of this contribution depends on a range of factors, including the silvicultural system and rotation length used, land degradation resulting from harvesting, reforestation, and the longevity of resultant forest products (e.g., Kurz et al. 1998; Harmon and Marks 2002). That the highest total forest C stocks are contained in the oldest forest stands is well established (Harmon et al. 1990; Smithwick et al. 2002), but it is also true that the age structure of Canada's conifer-dominated forests have been and (or) are currently being affected in profound ways by natural disturbance, climate change, and forest management. For example, fire suppression in many regions of Canada combined with long fire-return intervals in wetter areas, including many subzones within the Sub-Boreal Spruce (SBS) biogeoclimatic zone in central British Columbia, have led to increasingly old-aged stands (Kurz 2000), a situation that increases the likelihood that such forests are or may become sources for CO_2 as natural disturbances and harvesting and forest management activities occur (Kurz and Apps 1994).

In central British Columbia, various subzones of the SBS biogeoclimatic zone were recently found to contain as much as 47% old growth (defined as >140-year-old mean tree age), with 36% old growth overall (MacKinnon and Vold 1998), but with as little as 2.5% remaining in certain subzones (Burton et al. 1999). Many forces are currently creating a younger age structure. For example, many of the SBS stands dominated by older lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) are now coming under attack from pests such as bark beetles, which are subsequently being salvage logged. In fact, forest harvesting is the single most important factor now affecting stand age in SBS stands dominated by spruce (*Picea glauca* (Moench) Voss × *engelmannii* Parry ex Engelm.) (Kurz and Apps 1999), resulting in the conversion of largely old-growth stands into single-aged second-growth stands. With respect to annual wood volume harvest, recent figures (2002) show that nearly 40% of the total wood volume harvested in Canada was from British Columbia (NRCAN 2004), with 16% of the British Columbia total from the Prince George District alone (British Columbia Ministry of Forests 2004). As a result, forests are not only increasingly younger in these areas, but also more homogeneous in age and tree size, and snags and older trees are rarer (Wells et al. 1998). With the Kyoto Protocol recently ratified, there is an increasing need for ratifying nations such as Canada to understand the way in which forest management influences C stocks in forested regions.

Sub-boreal conifer forests of central British Columbia have been poorly studied with respect to C stocks, particularly those below ground. Based on prior measurements and modelling, we expected the significance of total C stocks, aboveground C stocks, and the relative importance of soil C to overall ecosystem C to be intermediate between that of coastal and boreal forests. For example, soil C : aboveground C ratios range from <1 (between 0.3 and 0.5 in Pacific Northwest coastal forests; Smithwick et al. 2002) to as high as 5 in boreal forests (Dixon et al. 1994). However, given the considerable uncertainty and range in these estimates, the significance of soils to total C storage in sub-boreal forests is very much in question. There is even less known about the way in which forest management might influence soil C stocks. Since clearcuts remain a source of CO_2 for up to 6 years after replanting (Pypker and Fredeen 2002*a*, 2002*b*), largely driven by elevated belowground respiration rates (Pypker and Fredeen 2002*b*), we assume that forest-floor and or soil C losses must be responsible for the fluxes. However, actual detection of soil C losses after harvesting has not been previously attempted for sub-boreal forests.

In this paper, we contrast the C stocks in old-growth SBS forests (minimum tree age >140 years) versus corresponding young, planted second-growth stands (minimum tree age <20 yeas) on soils of contrasting textures (coarse versus fine).

Materials and methods

This research was conducted in the UNBC–UBC Aleza Lake Research Forest (ALRF) located approximately 60 km east of Prince George (122°03′40″W, 54°03′11″N) in central sub-boreal British Columbia, Canada (Fig. 1). The ALRF lies within the wetter eastern portion of the SBS zone (SBSwk1 subzone; Delong 2003) and has a mean annual temperature of 3 °C and a mean annual precipitation of 930 mm (Jull 1992). Mature and old-growth forests are dominated by hybrid white spruce (*Picea glauca* × *Picea engelmannii*) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), with scattered veteran Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) on higher landscape positions, and occasional white birch (*Betula papyrifera* Marsh.) occupying canopy gaps. Second-growth stands established after clear-cut harvesting that began in 1980 were primarily replanted with seedlings of hybrid white spruce and secondarily with lodgepole pine (*Pinus contorta* var. *latifolia*).

Upland sites at the ALRF are underlain largely by fine-textured (silty clay loam to clay) glaciolacustrine deposits on which Luvisolic and associated Luvic Gleysolic soils have formed (Soil Classification Working Group 1998; Dawson 1989), equivalent to Boralfs and Aqualfs (Soil Survey Staff 1999). These soils are characterized by depletion of clay and some accumulation of organic matter in the surface A horizon, combined with distinct blocky structures in the much denser, clay-enriched Bt horizon (Arocena and Sanborn 1999). Roots are almost entirely confined to the forest floor and A horizons, which typically extend to a depth of 15–25 cm. Coarser textured (silt loam to loamy sand) glaciolacustrine and glaciofluvial sediments are found on less than 20% of the upland sites and are predominantly Orthic Humo-Ferric Podzols (Arocena and Sanborn 1999), with deeper root penetration evident. These two soil texture types will be referred to as fine and coarse, respectively, throughout this paper.

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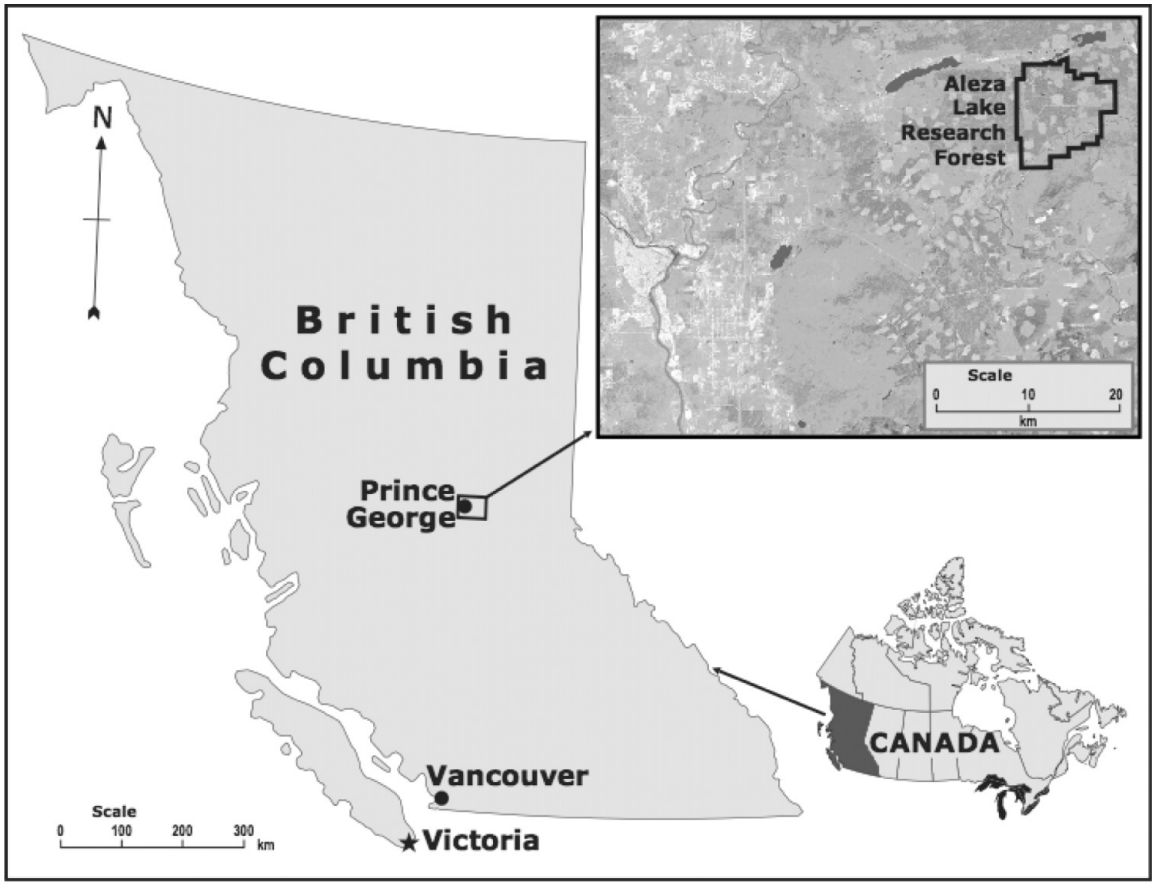
Fig. 1. Location of the Aleza Lake Research Forest within the province of British Columbia, Canada, with inset map of the Prince George area and research forest.



The ALRF has the longest documented record of forest management research in interior British Columbia, extending back to at least 1919. During this time, a wide variety of forest management activities have occurred in the forest, ranging from partial-cut systems such as diameter-limit logging to small- and large-patch clearcuts, with a variety of site preparation treatments including broadcast burning and mechanical scarification. As a result, the ALRF landbase as of 2003 was composed of 39% old-growth stands and 30% second-growth stands, almost all of which were harvested within the past 20 years, as well as smaller areas of partial cuts (19%).

Plot locations were selected randomly in 2003 within two forest inventory age-classes: 1, young, planted second-growth with dominant tree age between 0 and 20 years, and 8: old-growth primary forest with dominant tree age between 141 and 250 years, growing on either of the two dominant soil texture types (coarse and fine). Sites were positioned within the 7500-ha area of flat to gently undulating upland forest within the ALRF, which excluded river, lakes, floodplains, and riparian forest. In total, 27 young second-growth and 22 old-growth plots were established. Of the young second-growth plots, 20 were established on fine-textured soils and 7 on coarse-textured soils, while the composition of the 22 old-growth plots was 18 fine-textured and 4 coarse-textured sites. The smaller numbers of old-growth plots on the coarser soils reflected both the lesser occurrence of this soil type and a logging history that has favoured the higher volume stands available on these soil types. Thus, we limited the analysis in this paper to 4 plots each of (old-growth and young second-growth) × (coarse and fine-textured soils), for a total of 16 plots, using only those plots most similar in inferred soil moisture regime (mesic) and preharvest vegetation and site characteristics (Table 1). All sampling followed National Forest Inventory Sampling Guidelines (NFISG; Canadian Forest Inventory Committee 2002), unless specified otherwise.

Biomass C stocks

For each plot, large trees (≥1.3 m tall and ≥9.0 cm DBH) were measured nondestructively (diameter and species identification) over a 400-m^2 area surrounding the plot centre (Fig. 2). Height was estimated from DBH using allometric equations generated from ALRF permanent sampling plot data (C. Farnden and M. Jull, Prince George, British Columbia, unpublished data). Large-tree volumes and aboveground biomass components of foliage, stem bark, and stem wood were estimated using established allometric relationships of Penner et al. (1997) and Standish et al. (1985), respectively, and where necessary, Jenkins et al. (2003). Live total and fine root biomass was calculated using equations from Li et al. (2003).

Small trees and shrubs (≥1.3 m in height and <9.0 cm in basal diameter) were also nondestructively measured (diam-

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Table 1. UTM locations and soil profile and site characteristics of plots sampled for carbon at the Aleza Lake Research Forest in sub-boreal British Columbia.

Plot	UTM coordinates (zone 10)	Age-class and stand age	Soil texture	Slope, aspect (°, °)	Soil horizon thickness (cm) for upper 50 cm	Soil classification	Soil drainage
1	556387E, 5988505N	8, >140 years minimum tree age (old-growth)	Medium to coarse (silt loam to loamy sand)	5, 68	Ahe 6; Bf 44	Humo-Ferric Podzol – Eluviated Dystric Brunisols – Gleyed Podzolic Gray Luvisols	Imperfect, well drained
2	561988E, 5993678N			1, 180	Ahe 5; Bf 24; Bfj 21		
3	562569E, 5991088N			6, 315	Ae 17; Bf 11; Btg 22		
4	561004E, 5993199N			3, 71	Ae 20; Bf 13; Btg 17		
1	557162E, 5989447N	1, <20 years minimum tree age (young second-growth)	Medium to coarse (silt loam to loamy sand)	0, nil	Ah 7; Bf 8; Bfj 35	Humo-Ferric Podzol – Eluviated Dystric Brunisols – Gleyed Podzolic Gray Luvisols	Imperfect, well drained
2	556891E, 5989925N			0, nil	Ah 3; Bf 36;		
3	565423E, 5991473N			6, 308	Ahe 7; Bf 27; Btg 16		
4	565918E, 5991721N			1, 90	Ahe 8; Bf 24; Bfj 18		
1	561639E, 5990064N	8, >140 years minimum tree age (old-growth)	Fine (silty clay loam to clay)	1, 180	Ahe 5; Btg 45	Gleyed Gray Luvisols – Orthic Luvic Gleysols	Imperfect, poorly drained
2	561475E, 5991065N			2, 90	Ah 10; Bt 33; Btg 7		
3	559825E, 5993268N			5, 11	Ae 6; Bt 22; Btg 22		
4	564225E, 5991553N			0, nil	Ahe 13; Btg 37		
1	560653E, 5991732N	1, <20 years minimum tree age (young second-growth)	Fine (silty clay loam to clay)	2, 280	Ah 6; Bt 44	Gleyed Gray Luvisols – Orthic Luvic Gleysols	Imperfect, poorly drained
2	564384E, 5991421N			2, 333	Ae 16; Btg 34		
3	564453E, 5991670N			0, nil	Ahe 14; Btg 36		
4	565110E, 5991954N			1, 225	Ahe 6; Btg 44		

Note: Soil horizon nomenclature were taken from the Soil Classification Working Group (1998).

eter and species) over a smaller area (i.e., 50 m^2; Fig. 2), and total and component biomass for trees ranging from 2.5 to 9 cm DBH were estimated using Jenkins et al. (2003). Stemwood volumes of trees with DBH measuring <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).

C contents of tree biomass were estimated using the measured values of Lamlom and Savidge (2003). Shrub stem wood was determined using measured number of stems, mean stem height, and the measured average dimensions and density of individual stems. Woody shrubs (<1.3 m in height) and herbaceous plants were destructively harvested and accumulated separately within four 1-m^2 microplots located along transects (Fig. 2), and C contents were determined as explained next. Nonvascular plants (mosses, liverworts) and lichens, though functionally important, were not included because of their low contribution to C stocks (R. Botting, J. Campbell, and A. Fredeen, UNBC, unpublished data).

Woody debris C stocks

All woody debris stocks including tree stumps were evaluated. Coarse (>7.5 cm in diameter) and small (1.0–7.5 cm in diameter) woody debris as well as accumulations of piled downed wood referred to as "piled woody debris" in this paper) were estimated according to NFISG methods along two orthogonal 30-m transects (Fig. 2). Briefly, diameters and tilt angles of coarse woody debris pieces intersected by the transect were measured and the decay class of each piece was categorized into 1 of 5 decay classes ranging from lowest (intact bark, solid wood, round) to highest (barkless, twigless, soft or fragmented wood, oval). Total volume of coarse woody debris was calculated by a line-intersect method according to Van Wagner (1968, 1982) and Marshall et al. (2000) and converted to a mass basis using established decay class wood densities from the ALRF (D. Sachs, Forest Research Ecologist, Vancouver, British Columbia, unpublished data). All fine woody debris (≤1.0 cm in diameter) was sampled in four separately harvested 1-m^2 microplots concurrently with woody and herbaceous plant biomass (Fig. 2). Finally, tree stumps were enumerated and the diameter inside the bark, height, and percent sound wood recorded for each stump within a 4-m radius of the plot centre (Fig. 2). The C content of all woody debris, after correcting for density, was assumed to be 50% (Laiho and Prescott 1999).

Soil and forest-floor C stocks

Soil and forest-floor C stocks were sampled according to modified NFISG procedures, as indicated schematically in Fig. 3. Two belowground C pools, soil and forest floor, were measured directly. Soil C was estimated by subsampling 6.6-cm increments within two separate excavations to 46.6 cm depth within two plot quadrats in all plots and to 106.6 cm depth in approximately 25% of the plots (Fig. 3). Soil samples were obtained using a 9.6 cm inside diameter steel cylinder and slide hammer (Soilcon Laboratories, Richmond, British Columbia). Soil morphology, including soil texture, moisture regime, and drainage regime, was described from

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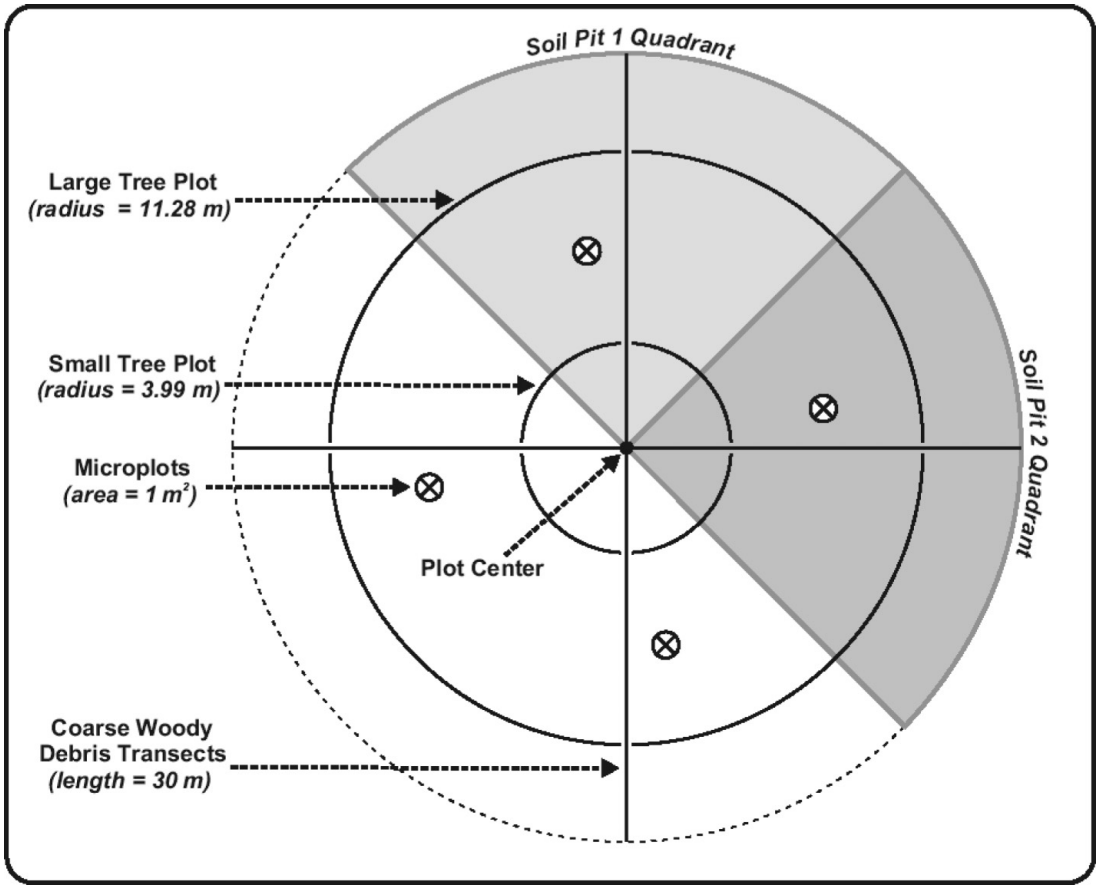
Fig. 2. Pictorial overview of the National Forest Inventory Sampling protocol used for sampling forest carbon stocks at the Aleza Lake Research Forest.



excavated pits (Soil Classification Working Group 1998; Meidinger 1998). Forest floor, including all litter and decomposed wood, was estimated at each site in 12 independent cores, three from each of the four microplots (Fig. 2). Cores were sampled using a fabricated coring bit (inside diam. 5 cm) mounted on a battery-driven power drill according to the design and specifications of Nalder and Wein (1998). Depth, dry mass, and bulk density of the mineral soil and forest-floor samples were measured. Individual core samples were analyzed separately but not considered separate replicates if from the same microplot. Stones were mostly absent from soils, representing ≤2% of the total sample mass. As a result, no corrections were made for their presence.

C content analysis

Forest-floor and soil samples were air dried, bulk densities determined, and subsequently ground to a fine powder using a coffee grinder followed by mortar and pestle. Woody biomass was ground to a fine powder using a hammermill (Micron Powder Systems; model W; Summit, New Jersey, USA). Subsamples (18–22 mg for mineral samples; 4–8 mg for biomass samples) of all ground or milled C stock samples were analyzed following the Dumas combustion method (Kirsten 1983) using an NA 1500 elemental analyzer (Fisons Instruments SP, Milano, Italy) for percent C determination. All samples were analyzed in duplicate, more if agreement was <95% between first and second subsamples. Total C concentration was taken as equivalent to organic C in all soil and biomass materials, although total C may have included unmeasured but likely minor amounts of charcoal in forest floors. Carbonates may occur in the fine-textured glaciolacustrine sediments, but at greater depths than were sampled in this study.

Statistical analysis

C stocks were tested for mineral soil texture, age-class, and their interaction effects using a two-way ANOVA in the PROC GLM procedures of SAS (SAS Institute Inc. 1989). With one minor exception, there were no texture or texture × age-class interaction effects for the C stocks measured. All main effects were considered significant at $\alpha = 0.05$. Means were compared using the Student–Newman–Keuls (SNK) test ($\alpha = 0.05$; SAS institute 1989). All C stock statistical analyses were performed on data expressed as C mass per hectare.

Results

Biomass C stocks

Total biomass C stocks were 3.6-fold (coarse-textured soils) and 3-fold (fine-textured soils) higher in old-growth stands than in young second-growth stands (Table 2). Stem, bark, branch, as well as total aboveground large-tree C

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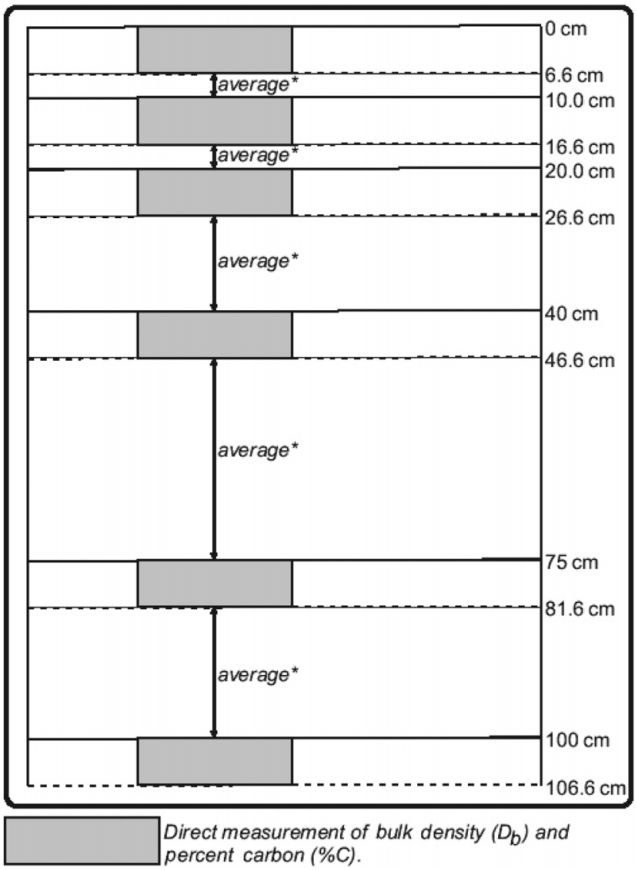
Fig. 3. Diagram of mineral soil core sampling for either 0–46.6 cm or 0–106.6 cm depth at the Aleza Lake Research Forest. Mineral soil carbon for nonsampled depth intervals (average*) was interpolated from levels within sampled depth intervals.



stocks were all greater in old-growth than in young second-growth stands on both soil types (Table 2). Large-tree stocks measured in the second-growth stands are the result of "leave"-tree patches intended to provide a legacy from primary forest stands, juvenile trees that were passed over during harvesting, and fast-growing hardwood species regrowing vegetatively. Stem-wood C stocks were 36% higher in old-growth forest growing on coarse- as opposed to fine-textured soils; however, this difference was not significant. All other measured biomass C stocks (herbaceous plants, shrubs, and small trees) were consistently higher, or in one case similar, in young second-growth stands relative to old-growth stands on a given soil type (Table 2). There were no significant differences between these same C stocks from similar age-classes on different soil types (Table 2). Allometric equations were used to calculate root biomass, which consisted mostly of large-tree roots in old-growth stands.

Woody debris C stocks

C stocks in coarse and fine woody debris were greater in old-growth as opposed to young stands (Table 3), but only coarse woody debris stocks on fine-textured soils were significantly elevated in old-growth versus second-growth stands. Though quantitatively small relative to woody debris stocks, piled woody debris and stumps showed the reverse trend in being numerically, but not significantly, larger in young second-growth than in old-growth stands (Table 3). Despite these opposing trends, total woody debris C stocks were between three and four times higher in old-growth than in young second-growth forests on similar soil types, which was significant for stands on fine-textured soils (Table 3).

Soil and forest-floor C stocks

Total mineral soil C stocks to 47 or 107 cm depths were 2%–6% lower in young second-growth stands relative to corresponding old-growth stands, though these differences were not significant. Mean mineral soil C stocks (to 47 cm depth) were higher (85 and 83 $Mg \cdot ha^{-1}$) in old-growth stands relative to young second-growth (83 and 78 $Mg \cdot ha^{-1}$) on coarse- and fine-textured soils, respectively (Table 4). Similar trends were observed for total mineral soil C to 107 cm depth. There were no significant effects of either age-class or texture on total mineral soil C to 47 cm or 107 cm depth (Table 4). Similarly, there were no significant differences between mineral soil C stocks by age-class or soil type at four depth intervals to 47 cm. Nevertheless, we observed numerically higher (30% (coarse) and 33% (fine)) mineral soil C stocks in old-growth versus second-growth stands in the surface soil layer (0–6.6 cm).

Mean forest-floor C stocks were larger in old-growth stands than in young plantations on comparable soil types and twice as high in old-growth on coarse versus fine-textured soils, but no differences were significant (Table 4). Forest-floor C stocks ranged from a high of 78 $Mg \cdot ha^{-1}$ to a low of 27 $Mg \cdot ha^{-1}$ in old-growth and younger second-growth stands on coarse-textured soils, respectively. Forest-floor C stocks were sizeable, equalling 68%–24% of the total C stocks contained in the mineral soils in these same stands.

Total forest C stocks were significantly higher in old-growth than in young second-growth stands on both soil types and 30% (not significant) higher in old-growth stands on coarse- as opposed to fine-textured soils (Fig. 4). Total forest C stocks ranged from a high of 423 $Mg \cdot ha^{-1}$ in old-growth on coarse-textured soils to a low of 193 $Mg \cdot ha^{-1}$ (fine) and 194 $Mg \cdot ha^{-1}$ (coarse) $Mg \cdot ha^{-1}$ in young plantations growing on the same soil type (Fig. 4). The significantly higher total forest C stocks in old-growth stands was largely driven by higher large-tree (i.e., canopy tree) biomass, forest floor, and woody debris (Tables 2–4).

Discussion

Total ecosystem C in upland old-growth sub-boreal stands at the ALRF ranged from 423 Mg $C \cdot ha^{-1}$ (coarse) to 325 Mg $C \cdot ha^{-1}$ (fine) (Fig. 4) between those found in old-growth forests of the Pacific Northwest (coastal and montane stands contain average total C stocks of 754–1127 $Mg \cdot ha^{-1}$; Smithwick et al. 2002) and those in boreal forests (e.g., stands in western Alberta contain an average of between 100 and 120 Mg $C \cdot ha^{-1}$; Banfield et al. 2002). It is clear that attempts to model and map C stocks for sub-boreal conifer forests of British Columbia would greatly underestimate C if boreal measurements were used, especially in the wetter and more productive sub-boreal forest subzones, such as those occurring at the ALRF.

Not unexpectedly, we found large-tree and total above-ground biomass C stocks to be significantly higher in old-

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Table 2. Mean (±SD) herb, shrub, small-tree (DBH < 9.0 cm; height >1.3 m), large-tree (DBH 9.0 cm; height >1.3 m) including biomass components, root, and total biomass (herb + shrub + small tree + large tree + root) C stocks by forest stand age and soil type at the Aleza Lake Research Forest in sub-boreal British Columbia.

	C stock (Mg C·ha^{-1})			Large-tree C stock (Mg C·ha^{-1})					C stock (Mg C·ha^{-1})	
Age-class, soil type	Herb	Shrub	Small tree	Stem wood	Stem bark	Foliage	Branch	Total	Total root	Total biomass
Old-growth, coarse	0.1±0.1a	5.3±7.0a	0.4±0.5a	116±48a	14±5a	7.3±4.0a	18±7a	155±63a	33±12a	195±71a
Second-growth, coarse	3.5±6.4a	6.5±6.9a	5.1±5.9a	17±26b	0.7±0.5c	0.7±0.5c	2±2c	20±27b	8±9b	42±45b
Old-growth, fine	0.2±0.2a	0.3±0.1a	2.3±1.6a	85±39a	10±4a	8.0±2.3a	16±6ab	119±50a	26±11a	149±61a
Second-growth, fine	0.3±0.3a	0.7±0.6a	1.4±1.3a	22±13b	3±2b	5.3±3.3ab	7±5bc	38±22b	9±5b	49±29b

Note: Means within a column sharing the same letter are not significantly different (Student–Newman–Keuls; $\alpha = 0.05$).

Table 3. Mean (±SD) coarse (7.5 cm in diameter), small (>1.0 cm and 7.5 cm in diameter), fine (>0 cm and 1.0 cm in diameter), and piled woody debris, stumps (diameter inside bark 4.0 cm), and total woody debris C stocks by forest stand age and soil type at the Aleza Lake Research Forest in sub-boreal British Columbia.

	C stock (Mg C·ha^{-1})					
Age-class, soil type	Coarse woody debris	Small woody debris	Fine woody debris	Piled woody debris	Stumps	Total woody debris
Old growth, coarse	32±19ab	1.0±0.1b	1.6±0.9a	0.19±0.34ab	0.00±0.00a	35±19ab
Second growth, coarse	10±7bc	0.8±0.3b	0.7±0.9a	0.43±0.21a	0.80±1.20a	13±7bc
Old growth, fine	27±3a	1.2±0.8ab	2.6±2.5a	0.02±0.03b	0.01±0.01a	31±2a
Second growth, fine	6±3c	1.3±0.2a	1.2±0.8a	0.14±0.10b	0.26±0.31a	9±4c

Note: Means within a column sharing the same letter are not significantly different (Student–Newman–Keuls; $\alpha = 0.05$).

Table 4. Mean (±SD) mineral soil, buried wood, and forest-floor C stocks (Mg C·ha^{-1}) by forest stand age and soil type at the Aleza Lake Research Forest in sub-boreal British Columbia.

	Soil C stock						
	Sampled interval (cm)				Pit total (cm)*		
Age-class, soil type	0–6.6	10–16.6	20–26.6	40–46.6	0–46.6	0–106.6	Forest-floor C stock
Old growth, coarse	24.6±9.8a	11.5±6.0a	8.0±6.1a	5.8±5.1a,b	85±20a	115±26a	78±54a
Second growth, coarse	18.8±9.7a	13.2±5.2a	10.2±5.9a	7.3±3.5a	83±22a	112±24a	27±6a
Old growth, fine	28.2±7.6a	14.7±6.4a	6.7±1.5a	3.1±0.9b	83±13a	110±16a	35±6a
Second growth, fine	21.2±5.5a	12.9±3.5a	9.5±3.0a	4.4±2.5ab	78±12a	106±17a	29±5a

Note: Means within a column sharing the same letter are not significantly different (Student–Newman–Keuls; $\alpha = 0.05$).
*Pit totals reflect the sum of C within sampled intervals as well as that C interpolated for nonsampled intervals (see Fig. 3).

growth than in young second-growth (age-class 1) stands on both soil types (Tables 2), as these trees were subject to removal by clear-cut harvesting within 20 years of sampling. All direct (e.g., Lee et al. 2002) as well as modeled (e.g., Harmon et al. 1990; Price et al. 1997) comparisons of aboveground C stocks that we are aware of demonstrate that old-growth or late-rotation forest stands have greater C in these stocks than in young or early- rotation stands. Old-growth aboveground biomass C at the ALRF amounted to 155 Mg·ha^{-1} on coarse soils and 119 Mg·ha^{-1} on fine-textured soils (Table 3), representing 96% and 97% of total aboveground biomass C, respectively. These totals are substantially higher than spatially averaged estimates for boreal forests in Canada, ranging from a low of 19 Mg·ha^{-1} (Botkin and Simpson 1990) to a high of 69 Mg·ha^{-1} (Houghton et al. 1983). In contrast, these aboveground biomass C totals for sub-boreal old-growth stands are much lower than similar estimates for old-growth coastal and montane forests in Oregon and Washington, ranging from 364 to 465 Mg·ha^{-1} (Smithwick et al. 2002).

Old-growth stands on coarse-textured soils had 30% higher total ecosystem (Fig. 4) and large-tree (Table 2) C stocks than old-growth stands growing on fine-textured soils (Fig. 4), a difference largely driven by greater forest-floor (123% higher) and large-tree (30% higher), and to a lesser extent by greater total woody debris (13% higher), C stocks (Tables 2–4). Higher (10%–40%) forest productivities and timber volumes contained in old-growth stands on coarse-textured soils have been reported (M. Jull, ALRF manager, unpublished data), a fact that has led to the current relative scarcity of old-growth stands on coarse-textured soils at the ALRF. The underlying, but as of yet unsubstantiated, reason for the higher forest C accumulations on coarse-textured soils at the ALRF may be related to higher site productivity resulting from improved drainage on coarse-textured soils in a region that has high levels of effective precipitation and relatively

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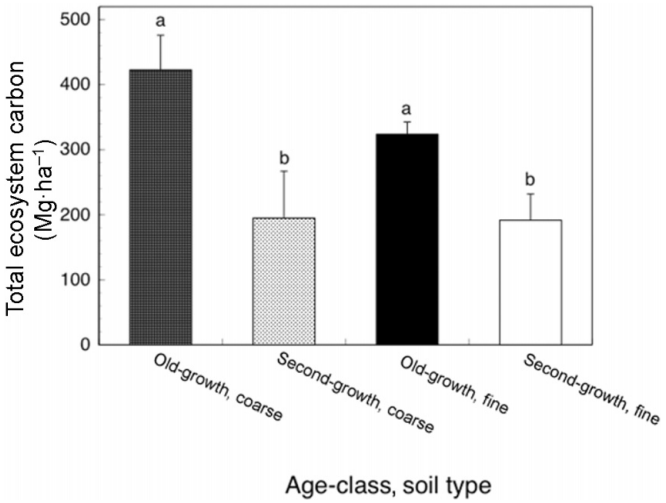
Fig. 4. Total ecosystem carbon on two soil types (coarse and fine) and two forest age-classes: old-growth (>140-year minimum tree age) and young second-growth (planted clear-cuts with <20-year minimum tree age) at the Aleza Lake Research Forest. Mean values (±SD) with similar letters indicate that they are not significantly different (Student–Newman–Keuls; $\alpha = 0.05$).



flat terrain with frequent ponding of water on fine-textured parent materials during spring and fall.

It is commonly assumed that soil and forest-floor C are reduced in the years following forest harvesting because of increased organic matter decomposition and reduced forest floor resulting from lower inputs of litter (Olsson et al. 1996; Pennock and van Kessel 1997). However, many studies have found only small changes in soil C (Johnson 1992) and belowground respiration (Pypker and Fredeen 2003) after harvesting. In the present study, we did observe a numerical but insignificant decrease of approximately 25% in mineral soil C content from old-growth to young second-growth stands in both soil types in the uppermost layer (0–6.6 cm depth), but not at greater soil depths. In fact, total soil C contents (0–47 or 107 cm depths) were overall quite uniform across age-class and soil type, with the younger stands in either soil type having only 2%–4% less total C (0–107 cm depth) than old-growth stands. These results are not artifacts of compaction of second-growth forest soils as a result of harvesting, since soil bulk densities were actually 10%–20% lower in second-growth stands on coarse-textured soils and unaffected on fine-textured soils. Thus, forest harvesting appears to have little effect on soil C beneath the forest floor and uppermost mineral soil horizons in sub-boreal spruce stands.

Total mineral soil C (to 107 cm depth) ranged from 110 to 115 $Mg \cdot ha^{-1}$ in old-growth stands at the ALRF. These values were within the range of that observed for boreal stands of central Canada (66–145 $Mg \cdot ha^{-1}$; Bhatti et al. 2002) and lower than mean soil C stocks found beneath coastal forests of Oregon (195 Mg $C \cdot ha^{-1}$) and Washington (365 Mg $C \cdot ha^{-1}$) (Smithwick et al. 2002). Total soil C stocks represented 54% (fine) to 57% (coarse) of the total C in young second-growth stands compared to 26% (coarse) to 33% (fine) of the total C in old-growth stands, similar to the 32%–35% of total ecosystem C found in soils in mature old-growth forests of coastal Oregon and Washington, respectively (Smithwick et al. 2002). In contrast, the proportion of ecosystem C in mineral soil C for boreal forests is more variable, ranging from 23% in more xeric montane stands of west-central Alberta (Banfield et al. 2002) to 85% for hygric black spruce forests of central Saskatchewan (Malhi et al. 1999).

Mean forest-floor C stocks were 65% (coarse) and 17% (fine) lower in young second-growth stands relative to old-growth stands. However, because of high levels of spatial variability in these stocks, a problem commonly encountered in forest-floor studies (Yanai et al. 2003), differences were not significant. Nevertheless, the trend is suggestive of a decline in forest floor after harvest, consistent with the large decrease in litter inputs following removal of the tree canopy combined with unaffected rates of litter decomposition seen in other spruce–fir forests (Lytle and Cronan 1998). Mean forest-floor C stocks found in the present study for old-growth stands ranged from 35 $Mg \cdot ha^{-1}$ (fine) to 78 $Mg \cdot ha^{-1}$ (coarse), higher than the 25–34 $Mg \cdot ha^{-1}$ mean levels found in boreal forests (Bhatti et al. 2002) and the 12–22 $Mg \cdot ha^{-1}$ mean levels found in montane and coastal forests of the Pacific Northwest (Smithwick et al. 2002).

Woody debris C stocks, though smaller in magnitude in all cases than corresponding forest-floor stocks, showed the same general trend in having lower levels in second-growth than in old-growth stands. Coarse woody debris C stocks ranged from 35 $Mg \cdot ha^{-1}$ (coarse) and 31 $Mg \cdot ha^{-1}$ (fine) in old growth to 13 $Mg \cdot ha^{-1}$ (coarse) and 9 $Mg \cdot ha^{-1}$ (fine) in new second growth. The range of mean woody debris stocks in old-growth stands in this study was 13–52 $Mg \cdot ha^{-1}$ (coarse) and 22–30 $Mg \cdot ha^{-1}$ (fine), corresponding to 119–540 $m^3 \cdot ha^{-1}$ (coarse) and 248–359 $m^3 \cdot ha^{-1}$ (fine) of woody debris volume. Volumes permit greater comparison with literature values where conversion to C stocks was not performed. The range of woody debris volume on our old-growth sites was higher than a published range for the same biogeoclimatic zone in British Columbia (SBSwk: 21–101 $m^3 \cdot ha^{-1}$) (Densmore et al. 2004) and within the range of values given for an adjacent zone (SBSmk: 41–532 $m^3 \cdot ha^{-1}$) (Feller 2003). In a broader geographical context, total woody debris C stocks in sub-boreal stands were only one-third to one-half as large as those in coastal temperate forests of the Pacific Northwest (Smithwick et al. 2002).

Models generally predict decreases in belowground C (taken as all stocks below ground level) with forest harvesting for cordilleran forests of western Canada (Price et al. 1997; Seely et al. 2002), which at least in terms of the direction of change matched results reported here. However, the three components that make up total belowground C (mineral soil + forest floor + roots) in this study were not affected equally. Mineral soil C was not significantly affected by age-class (forest harvesting) or soil type, and absolute differences in mineral soil C stocks between age-classes and even soil types were small. Forest-floor levels showed greater relative and absolute differences than soil C stocks between old growth and young plantations, but were also not significant. Finally, total live large-root C estimates, mostly in the form of large-tree roots, were significantly greater in old-growth on both coarse- and fine-textured soils. However, live tree root C was not estimated directly in this study, but rather by allometric equations. These equations likely pro-

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vide conservative estimates, assuming 22% of the biomass was in live roots, lower than the 25% measured in 142-year-old Norway spruce stands in Germany (Mund et al. 2002). Dead root C was not estimated in this study and therefore differences between old-growth and young plantations could be less than shown. While the rate of decomposition for coarse roots is unknown for our study area, if we assume mass loss rates similar to those obtained for coarse woody debris in Canadian Rocky Mountain (Laiho and Prescott 1999) or Russian (Krankina et al. 2002) spruce forests, 80%–90% of the coarse root C might be presumed to be lost after 20 years. If it is further assumed that young stands start with old-growth large-root C at time of harvest, 33 $Mg \cdot ha^{-1}$ (coarse) and 26 $Mg \cdot ha^{-1}$ (fine), the residuals from these stocks would range from 6.6 to <3 Mg $C \cdot ha^{-1}$. While we can not have great confidence in these estimates, we feel it is safe to project that any legacy of large-tree root carryover to soils of young second-growth stands is likely to be negligible in the context of the relatively long rotation ages and the magnitudes of the overall ecosystem C stocks of sub-boreal forests.

Conclusions

Sub-boreal forests of central British Columbia appear to be intermediate with respect to both aboveground and total C stocks between the wetter and more productive coastal forests to the south and west and the less productive boreal stands to the north and east. Aboveground C stocks, mostly large-tree stocks, were the largest single C stock in old-growth stands and represented a majority of the C lost following conversion of old growth to young plantation. However, woody debris C stocks were also significantly reduced following conversion of old-growth stands to young plantations in both coarse- and fine-textured soil types. There were also significant decreases in forest floor on fine-textured sites. While the size of mineral soil C stocks were second only to large-tree stocks, it was not significantly affected by harvesting, despite apparent losses of C in the uppermost soil layer. If we are to manage for C stocks along with other forest values, cognizance and conservation of the legacy of nonbiomass C stocks in our old-growth forests (i.e., woody debris and forest floor) could well be important in our attempts to minimize greenhouse gas contributions resulting from sub-boreal forest management activities.

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References

Arocena, J.M., and Sanborn, P. 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.

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.

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

British Columbia Ministry of Forests. 2004. Forest regions and districts [online]. Available from http://www.for.gov.bc.ca/mof/regdis.htm [accessed 11 July 2004].

Burton, P.J., Kneeshaw, D.D., and Coates, K.D. 1999. Managing forest harvesting to maintain old growth in boreal and sub-boreal forests. For. Chron. **75** (4): 623–631.

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 11 May 2004].

Dawson, A.B. 1989. Soils of the Prince George – McLeod Lake area. British Columbia Ministry of the Environment, Victoria, B.C. Tech. Rep. No. 29.

DeLong, C. 2003. A field guide to site identification and interpretation for the southeast portion of the Prince George Forest Region. British Columbia Ministry of Forests, Victoria, B.C. Land Manage. Handb. No. 51.

Densmore, N., Parminter, J., and Stevens, V. 2004. Coarse woody debris: inventory, decay modelling, and management implications in three biogeoclimatic zones. British Columbia Journal of Ecosystems and Management, **5**(2):14–29.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science (Washington, D.C.), **263**: 185–190.

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

Gates, D.M. 1993. Climate change and its biological consequences. Sinauer Associates, Inc., Sunderland, Mass.

Harmon, M.E., Ferrell, W.K., and Franklin, J.F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science (Washington, D.C.), **247**: 699–702.

Harmon, M.E., and Marks, B. 2002. Effects of silvicultural practices on carbon stores in Douglas-fir – western hemlock forests in the Pacific Northwest, U.S.A.: results from a simulation model. Can. J. For. Res. **32**: 863–877.

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.

IPCC. 2000. Land use, land-use change and forestry. Summary for policymakers. World Meteorological Organization and United Nations Environment Programme. IPPC, Geneva.

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.

Johnson, D. 1992. Effects of forest management on soil carbon stores. Water Air Soil Poll. **64**: 83–120.

© 2005 NRC Canada

Jull, M. 1992. Aleza Lake Research Forest: management and working plan No. 1. British Columbia Ministry of Forests, Prince George, B.C.

Karnosky, D.F. 2002. Impacts of elevated atmospheric CO_2 on forest trees and forest ecosystems: knowledge gaps. Environ. Int. **29**: 161–169.

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

Krankina, O.N., Harmon, M.E., Kukuev, Y.A., Treyfeld, R.F., Kashpor, N.N., Kresnov, V.G. et al. 2002. Coarse woody debris in forest regions of Russia. Can. J. For. Res. **32**: 768–778.

Kurz, W.A. 2000. Boreal forest carbon budgets. *In* Proceedings of the International Science Conference on The Role of Boreal Forests and Forestry in the Global Carbon Budget, 8–12 May 2000, Edmonton, Alta. *Edited by* M.J. Apps and J. Marsden. Canadian Forest Service, Natural Resources Canada, Ottawa. p. 2.

Kurz, W.A., and Apps, M.J. 1994. The carbon budget of Canadian forests: a sensitivity analysis of changes in disturbance regimes, growth rates, and decomposition rates. Environ. Pollut. **83**: 55–61.

Kurz, W.A., and Apps, M.J. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Appl. **9**(2): 526–547.

Kurz, W.A., Beukema, S.J., and Apps, M.J. 1998. Carbon budget implications of the transition from natural to managed disturbance regimes in forest landscapes. Mitigation and Adaptation Strategies for Global Change, **2**: 405–421.

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.

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.

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.

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.

Lytle, D.E., and Cronan, C.S. 1998. Comparative soil CO_2 evolution, litter decay, and root dynamics in clearcut and uncut spruce–fir forest. For. Ecol. Manage. **103**:121–128.

MacKinnon, A., and Vold, T. 1998. Old-growth forests inventory for British Columbia, Canada. Nat. Areas J. **18** (4): 309–318.

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.

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

Meidinger, D. 1998. Field manual for describing terrestrial ecosystems [online]. British Columbia Ministry of Environment, Land, and Parks and British Columbia Ministry of Forests, Victoria, B.C. Land Management Handbook 25. Available from http://www.for.gov.bc.ca/hfd/pubs/Docs/Lmh/Lmh25.htm [accessed 11 July 2005].

Mund, M., Kummetz, E., Hein, M., Bauer, G.A., and Schulze, E.-D. 2002. Growth and carbon stocks of a spruce forest chronosequence in central Europe. For. Ecol. Manage. **171**: 275–296.

Natural Resources Canada. 2004. The state of Canada's forests: 2003–2004 [online]. Available from http://www.nrcan.gc.ca/cfs-scf/national/what-quoi/sof/latest_e.html [accessed 11 July 2004].

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.

Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., and Rosen, K. 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. For. Ecol. Manage. **82**: 19–32.

Penner, M., Power, K., Muhairwe, C., Tellier, R., and Wang, Y. 1997. Canada's forest biomass resources: deriving estimates from Canada's forest inventory. Can. For. Serv. Pac. For. Res. Cent. Inf. Rep. BC-X-370.

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.

Prentice, I.C., Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heimann, M., Jaramillo, V.J. et al. 2001. The carbon cycle and atmospheric carbon dioxide. *In* Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson. Cambridge University Press, Cambridge, UK.

Price, D.T., Halliwell, D.H., Apps, M.J., Kurz, W.A., and Curry, S.R. 1997. Comprehensive assessment of carbon stocks and fluxes in a Boreal-Cordilleran forest management unit. Can. J. For. Res. **27**: 2005–2016.

Pypker, T.G., and Fredeen, A.L. 2002*a*. The growing season carbon balance of a sub-boreal clearcut five years after harvesting using two independent approaches to measure ecosystem CO_2 flux. Can. J. For. Res. **32**: 852–862.

Pypker, T.G., and Fredeen, A.L. 2002*b*. The growing season carbon balance of a sub-boreal clearcut five and six years after harvesting. Agric. For. Meteorol. **114**(1): 15–30.

Pypker, T.G., and Fredeen, A.L. 2003. Below ground CO_2 efflux from cut blocks of varying ages in sub-boreal British Columbia. For. Ecol. Manage. **172**: 249–259.

Schulze, E.-D., Wirth, C., and Heimann, M. 2000. Managing forests after Kyoto. Science (Washington, D.C.), **289**: 2058–2059.

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

SAS Institute Inc. 1989. SAS/STAT user's guide version 6, 4th ed. [computer manual]. SAS Institute Inc., Cary, N.C.

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

Soil Survey Staff. 1999. Soil taxonomy. 2nd ed. USDA Agric. Handb. 436.

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.

Standish, J.T., Manning, G.H., and Demaerschalk, J.P. 1985. Development of biomass equations for British Columbia tree species. Can. For. Serv. Pac. For. Res. Cent. Inf. Rep. BC-X-264.

© 2005 NRC Canada

Thornley, J.H.M., and Cannell, M.G.R. 2000. Managing forests for wood yield and carbon storage: a theoretical study. Tree Physiol. **20**: 477–484.

Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S. et al. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needle-leaf forests. Agric. For. Meteorol. **113**: 185–222.

Van Wagner, C.E. 1968. The line-intercept method in forest fuel sampling. For. Sci. **14**: 20–26.

Van Wagner, C.E. 1982. Practical aspects of the line intersect method. Can. For. Serv. Petawawa Natl. For. Inst. 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.

Yanai, R.D., Stehman, S.V., Arthur, M.A., Prescott, C.E., Friedland, A.M., Siccama, T.G., and Binkley D. 2003. Detecting change in forest floor carbon. Soil Sci. Soc. Am. J. **67**: 1583–1593.

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