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Carbon and biomass partitioning in balsam fir (*Abies balsamea*)

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Summary Balsam fir (*Abies balsamea* (L.) Mill) was extensively sampled to investigate the effects of forest management practices, site location, within-crown position, tree component (i.e., stem, foliage, branches and roots), and tree social classes on biomass and carbon (C) partitioning at the individual tree level and across ecological regions. The sites were located in three ecologically distinct forest regions of west-central New Brunswick, Canada. There were no significant differences in %C content of trees across ecological regions or across tree social classes. However, at the individual tree level, significant differences were evident in biomass and C allocation between different parts of the tree, between treatment types (i.e., unmanaged and pre-commercially thinned stands) and between within-crown positions, indicating the need for separate estimates of biomass and C content of tree components to obtain more precise estimates of quantities at the stand level. Calculating stand C content based on constant allocation values, as is commonly done, produced errors of up to 15% compared with the values calculated in this study. Three allometric equations of biomass and C that account for partitioning among different parts of the tree were developed and compared: (1) a third-order polynomial, (2) a modified inverse polynomial and (3) a modified Weibull equation. Diameter at breast height (DBH) was used as the only explanatory variable to describe fresh biomass, dry biomass and C content. All regressions derived showed a high correlation with DBH, with most r^2 values > 0.95. A comparison of the equation results showed that the modified Weibull equation gave consistent results with the best overall fit and was the simplest of the three equations investigated. The regressions can be used to estimate forest biomass and tree C content at the stand level, given specific information on DBH.

Keywords: allometric equations, carbon content, dry biomass, eco-region, fresh biomass, unmanaged stands, pre-commercially thinned stands, regression equations, social classes.

Introduction

As the largest terrestrial ecosystem, forests play a significant role in the balance of the global carbon (C) cycle and in the long-term storage (sequestration) of C (Keeling and Whorf 1996, Barr et al. 2002, Lamlom and Savidge 2003) by absorbing substantial amounts of C from the atmosphere and storing it in their tissues and in soils (Birdsey 1992, Liski et al. 2001). Accurate and precise measurements of C sequestered and stored in forests are required to fully understand the role of forests in the global C cycle, particularly in mitigating CO_2 emissions (Brown 2002). Policy incentives, including those associated with commitments to the United Nations Framework Convention on Climate Change and obligations under the Kyoto Protocol (IPCC 2001), for measuring C in forests have gained some international acceptance (Good et al. 2001, Brown 2002). One response to such obligations in Canada was the recent (2002) establishment of Fluxnet-Canada to investigate the role of commercial forests in the annual exchange of CO_2 and the sequestration of atmospheric C.

A national inventory reference to forest C must be established to investigate the relationships between CO_2 emission and its subsequent removal by forests as a result of management actions such as pre-commercial thinning, commercial harvesting, deforestation and afforestation. To start such an inventory, the content of C, which is species-specific, has to be determined (Gower et al. 1997). Although there have been several studies determining the C content of trees, there are few data sets relating C content to entire forests (e.g., Mingle and Boubel 1968, Reichle et al. 1973, Chow and Rolfe 1989, Lamlom and Savidge 2003) because special effort is needed to estimate C content at the stand to forest level (Brown et al. 1997, 1999, Schroeder et al. 1997, Brown and Schroeder 1999, Bond-Lamberty et al. 2002). Differences in %C among different tree species and among wood types within a single tree (Barton 1984, Lamlom and Savidge 2003) indicate the need to estimate biomass and C content for each species and each tree component. Most published studies on this subject, however, have focused on total aboveground biomass and C, whereas discrimination among the different parts of the tree, wood types, and stocking densities by age and volume classes (Barton 1984), is rarely done.

Based on field measurements of biomass, a constant biomass expansion factor (BEF; a ratio of total aboveground biomass to merchantable volume) is often used to convert merchantable volume to total aboveground biomass (Brown et al. 1997, 1999, Brown and Schroeder 1999). In turn, 50% of the dry biomass of trees is often used as the estimate of the C content in trees. However, Lamlom and Savidge (2003) have demonstrated that the amount of C in wood varies with wood type (juvenile versus heartwood), tree type (softwood versus hardwood), tree species, tree genotype and geographical location. Moreover, use of the constant multiplier is imprecise because the BEF is not a constant, but varies exponentially, in a decaying fashion, with increasing merchantable volume (Joosten et al. 2004).

Allometric equations that relate mensurational variables like diameter at breast height (DBH) to variables that are more difficult to measure are often used to estimate stand biomass and volume (Brown et al. 1999, Brown 2002). Gower et al. (1997) have recently updated biomass equations for mature trembling aspen (*Populus tremuloides* Michx.), mature black spruce (*Picea mariana* (Mill.) BSP) and young-to-mature jack pine (*Pinus banksiana* Lamb.) stands in Saskatchewan and Manitoba, and there is no shortage of allometric equations in the literature relating stem diameter to tree biomass and cross-sectional sapwood area (e.g., Smith and Brand 1983, Penner et al. 1997, Ter-Mikaelian 1997, Bond-Lamberty et al. 2002, Jenkins et al. 2003, 2004). However, no allometric equations have been developed specifically for the determination of biomass and C in balsam fir (*Abies balsamea* (L.) Mill). Also, most of the existing allometric equations for biomass are based on trees harvested in the late 1960s to early 1980s (Baskerville 1965, Ker and van Raalte 1981, Freedman et al. 1982, Brown et al. 1997), and may not reflect current growing conditions. As well, the inherent differences in biomass and C allocation among the different parts of the tree were seldom investigated (Gower et al. 1995).

The objectives of our study were to: (1) determine the C content of the different parts of balsam fir trees; (2) determine what influence forest management practices, study site location (as it relates to climate), and within-crown position have on the C content of balsam fir; (3) develop allometric equations for biomass and C content of balsam fir; and (4) compare the results generated by three separate regression equations to the measured biomass and C content data.

Methods

Study sites

The study was conducted at three climatically distinct forest locations, namely (1) Charlie Lake, (2) Nashwaak Lake and (3) the Acadia Research Forest (Figure 1). Each location is within a different ecological region of New Brunswick (NB), Canada (Ecological Classification Working Group 2003). Growing conditions at each study area are given in Table 1. The study sites consist of 20–40-year-old balsam fir stands that have originated from clear-cut harvesting. Portions of these stands underwent pre-commercial thinning between 12 and 15 years ago.

The Charlie Lake site is located in central NB (45°53′5″ N, 67°21′25″ W) at an elevation of 153 m a.s.l. The site is located in the Valley Lowlands eco-region (Ecological Classification Working Group 2003), which is characterized by a relatively dry, warm climate. Mean annual air temperature for the growing season is 13.5 °C, and mean annual rainfall is 1194 mm. Mean number of growing degree days is 1583. The soil is a well-drained sandy loam, with a mean duff thickness of 6–7 cm. The forest is predominantly composed of sugar and red maple (*Acer saccharum* Marsh., *Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), red spruce (*Picea rubens* Sarg.), balsam fir (~90% of the total site volume), eastern white pine (*Pinus strobus* L.) and hemlock (*Tsuga canadensis* (L.) Carr.).

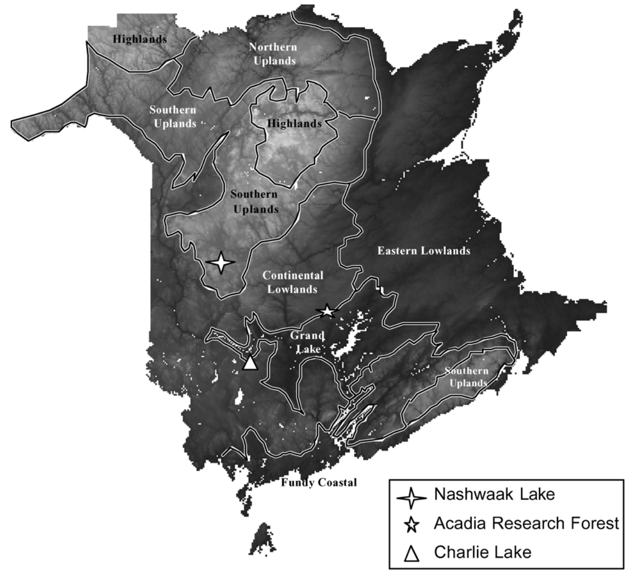

Figure 1. Study site location and ecological regions of New Brunswick.

The Nashwaak Lake site is located in central NB (46°28′20″ N, 67°06′0″ W). The site is in hilly terrain with elevations ranging from 320 to 350 m. The site is located in the Central Uplands eco-region (Ecological Classification Working Group 2003), which is characterized by warm, rainy summers and mild, snowy winters. Mean annual air temperature for the growing season is 10.8 °C. Mean annual rainfall is 1392 mm. Mean number of growing degree days for this region is about 1302. The soil is a well-drained sandy loam, with a mean duff thickness of 6–7 cm. The site is rocky with some large boulders interspersed. Mixed-wood forest in the region is primarily composed of sugar and red maple, red spruce, white spruce (*Picea glauca* (Moench) Voss) and balsam fir. Balsam fir comprises more than 95% of the total site volume.

The Acadia Research Forest site is located in central NB (45°59′24″ N, 66°18′36″ W) with elevations ranging from 30 to 60 m. The site is situated in the Grand Lake Lowlands eco-region (Ecological Classification Working Group 2003), which is characterized by a warm, dry climate. Mean annual air temperature for the growing season is 14.6 °C. Mean an-

Table 1. Description of the study areas. Abbreviations: PCT = pre-commercially thinned areas; and UN = unmanaged areas.

Site (treatment)	Forest age	Basal area ($m^2\ ha^{-1}$)	Density (stems ha^{-1})	Mean height (m)	Mean DBH (cm)
Charlie Lake (PCT)	20–25	30	2238	12.0	15.1
Charlie Lake (IUN)	20–25	33	22,200	6.9	3.7
Nashwaak Lake (PCT)	32–37	26	1950	13.5	16.4
Nashwaak Lake (UN)	32–37	43	13,400	9.6	5.4
Acadia (PCT)	35–40	24	3383	14.3	18.0
Acadia (UN)	35–40	42	19,166	8.4	4.8

nual rainfall is 1143 mm. Mean number of growing degree days for this region is estimated to be between 1700 and 1800. The soil is a compact clay loam. The lack of relief in the area as well as high soil clay content often impedes drainage. The region supports a wide range of tree species including bur oak (*Quercus macrocarpa* Michx.), ironwood (*Ostrya virginiana* (Mill.) K. Koch), basswood (*Tilia americana* L.) and silver maple (*Acer saccharinum* L.), which are incapable of growing in the cooler regions of the province. At the sampled site, trees were predominantly balsam fir (~95% by volume).

At each study location, a stand was selected that contained unmanaged (UN) and pre-commercially thinned (PCT) sections to determine the influence of forest management practices on biomass allocation and tissue C content. The study was designed to investigate both tree-level and stand-level attributes. Therefore, to capture detail at both scales, three 0.04-ha permanent sample plots (PSPs) were established near where the sample trees were felled. Because a commercial thinning study was planned for the Acadia Forest study site, nine 0.04 ha PSPs were used. Approximately 2–3 trees per 4-cm diameter class (eight trees for most sites) were selected. The information recorded for each of the sample trees was the same as that collected at each of the PSPs and included co-ordinate position (GPS reference number), diameter class, DBH, mean crown width, and social class, i.e., dominant (D), co-dominant (CD), intermediate (I), suppressed (S) and regeneration (R) designations, after Husch et al. (2003).

Aboveground sampling

Field sampling and measurements After felling each sample tree, tree height was measured from the cut stem base to the top of the crown. The height to the first living branch was recorded as the height of the live crown. The trees were then divided into three equal crown portions: upper, middle and lower. The length of the longest branch in each portion was measured and recorded. All branches were then cut from the tree as close to the main stem as possible with a chainsaw or pruning shears. Dead and live branches in each crown portion were collected and weighed separately. Three representative branches from each crown portion were selected, placed in labeled plastic bags and transported to the Canadian Forest Service, Atlantic Forestry Centre (CFS-AFC, Fredericton, NB) where they were stored at –20 °C until they could be oven-dried and analyzed for C.

After removing and sampling the branches, a series of wood disks (1 cm thick) were cut at 0.15 (stump height), 1.0, 1.37 (DBH height) and 2 m, and then every meter along the main stem to the top of the tree. Tree and disk information were labeled on the back of each disk. These disks were placed in labeled plastic bags and stored at –20 °C at the CFS-AFC until they could be further processed.

Laboratory analysis For each branch sample, the total length (cm) and mid-length diameter (mm) were measured. Each branch was then cut into smaller portions, which were placed in paper bags and the total fresh mass of the branch determined. The bags were then weighed after drying to a constant mass at 70 °C.

Needles were separated from the dried branches and placed in paper bags and dried for another 1 to 2 days and then weighed.

Foliage and branch samples were pulverized in a Wiley mill (Brabender, Duisburg, Germany) to pass a 2-mm screen. The ground samples were placed in labeled coin envelopes and held in the drying oven until analyzed for C content.

Root sampling

The roots of 12 sample trees, eight from the pre-commercially thinned stand and four from the unmanaged portion of the same stand at the Acadia Research Forest study site, were excavated with a backhoe. Root systems were transported to the headquarters of the Acadia Research Forest and washed free of soil. Within several days, the fresh mass of the entire root system was determined with an OHAUS digital scale (Ohaus, Pine Brook, NJ).

Five major lateral roots were sampled from the main tap root of each root clump. These lateral roots were based on the mean diameter of all lateral roots of that clump, and the fresh mass of each sample was determined. The root samples were then transported to CFS-AFC, dried to constant mass at 70 °C and ground with a Wiley mill.

C content

The C present in each tissue sample was determined with a CNS-2000 Elemental Analyzer (LECO, St. Joseph, MI).

Statistical analysis

Biomass and C content differences among tree components, within-crown positions, thinning treatments, sites and social classes were evaluated by single-factor analysis of variance (ANOVA). The experimental unit was the sample tree, which was selected according to the diameter classes identified from PSP measurements. Study region, social class, tree component and within-crown position were treated as fixed effects. All statistical analyses were carried out with SPSS Version 11.5 program software (SPSS Science, Chicago, IL).

Results and discussion

Distribution pattern of tree C

Percentage C variation among different parts of the tree The %C in branches, foliage, stems and roots for all sites averaged (± SD) 52.40 ± 1.31, 52.92 ± 0.98, 51.87 ± 0.99 (ranging from 49.20 to 53.89% in the 27 samples investigated) and 49.72 ± 1.39%, respectively (Figure 2). The %C differed significantly between tree components (single-factor ANOVA: $F_{3,\ 228}$ = 75.92, $P < 0.0001$, within group degrees of freedom (DF) = 228, mean square variance (MS) = 1.44, and between group DF = 3, MS = 109.58). Carbon content was highest in foliage, lowest in roots and slightly lower in stems than in branches. Lamlom and Savidge (2003) investigated the C content of heartwood of balsam fir and reported values of 50.08 ± 0.45% (SD) compared with our stem value of 51.87%. This difference was statistically significant (i.e., $t_{3,58} = 5.42$; where $t_{crit} = 2.18$ at $\alpha = 0.05$). Lamlom and Savidge's (2003) samples were taken from planed and sawn blocks of kiln-dried clear heartwood, whereas our wood sampling method did not specifically select for either earlywood or heartwood. Percent C in the crown, including branches and foliage, was 0.53–1.05% (mean 0.76%) higher than in the stem. Our mean value corresponded well with the value of 0.75% reported by Joosten and Schulte (2002).

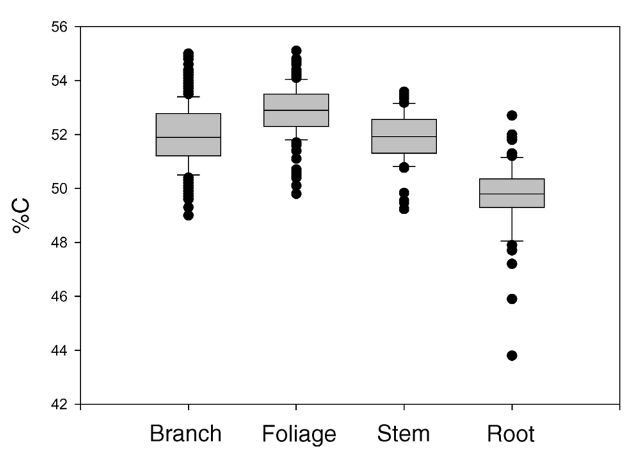

Figure 2. Percent carbon (%C by dry mass) of the different parts of a balsam fir tree. The filled circles represent outliers; the vertical bars represent data ranges defined as 1.5 × the inter-quartile range; the horizontal lines within the boxes represent median values; and the upper and lower bounds of the boxes represent the 3rd and 1st quartiles, respectively.

Percentage C variation among sections of the tree crown
Figure 3 shows that mean differences in %C among the lower, middle and upper portions of the sampled trees were statistically significant for the branches (single-factor ANOVA; $F_{2,484}$ = 8.17, $P < 0.0001$, $F_{crit} = 3.34$; Figure 3a(1)), foliage ($F_{2,\ 188}$ = 4.15, $P < 0.017$, $F_{crit} = 3.34$; Figure 3b(1)) and stems ($F_{3,\ 189}$ = 3.39, $P < 0.0001$, $F_{crit} = 3.34$; Figure 3c(1)). Similar variation was found for the branches and stems, with %C increasing from the top to the base of the crown by 0.6 and 0.8% for branches and stems, respectively. The foliage in the middle section of the tree had the highest %C, whereas foliage in the upper section of the tree had the lowest %C. The %C change in the foliage from the top to the lower sections of the crown can be attributed to different growing conditions because leaves at different levels in the crown may be subjected to different irradiances and availabilities of nutrients and water (Zha et al. 2002) that result in differences in specific leaf area (Jordan and Smith 1993, Ishii et al. 2002), photosynthetic activity (Hollinger 1989, Evans 1993, Hollinger et al. 1993), leaf nitrogen (N) (Hirose and Werger 1987, Hollinger 1989, Evans 1993) and dark respiration rates (Zha et al. 2002). The increases in %C in branches and stems from the upper to the lower sections of the tree may be explained by differences in the ratio between twigs and branches at different levels within the crown, and consequently to different ratios of heartwood to sapwood (cf. Lamlom and Savidge 2003).

Percentage C variation and stand thinning Thinning had a significant effect on stem %C (single-factor ANOVA; $F_{1,\ 194}$ = 13.32, $P < 0.0001$; Figure 3c(2)), indicating that pre-commercial thinning can increase %C of stems by 0.86%. The difference in branch %C between the UN and PCT stands was also significant ($F_{1,\ 485}$ = 4.19, $P = 0.041$; Figure 3a(2)), with %C 0.24% lower in thinned stands than in unthinned stands. The %C in foliage showed no significant difference between thinning treatments ($F_{1,\ 189}$ = 0.09, $P = 0.765$; Figure 3b(2)). Thinning improves light conditions in the stand, and the increase in irradiance increases the shoot:root ratio, leading to rapid aboveground growth, which in turn, increases shoot demand for N and other mineral nutrients. This may increase photosynthate flow to the stem for storage and to the roots for root expansion, thereby decreasing the %C in the branches and slightly increasing the %C in the stem and roots (Cannel and Dewar 1994, Mailard et al. 1999, Lacointe 2000, Le Roux et al. 2001). Lavigne (1991) reported increased allocation of photosynthates to branches and roots in trees sampled from pre-commercially thinned balsam fir stands compared with those sampled from unmanaged stands. These results support the conclusions of Grigal and Ohmann (1992) that C storage in forests is influenced by forest management activities. It is expected that other management practices such as applying fertilizers and other growth enhancers will also affect tree C content.

Percentage C variation among study regions Mean %C content of branches and stems did not differ significantly between study sites, with $F_{2,\ 484}$ = 2.24, $P = 0.108$ for branches (Fig-

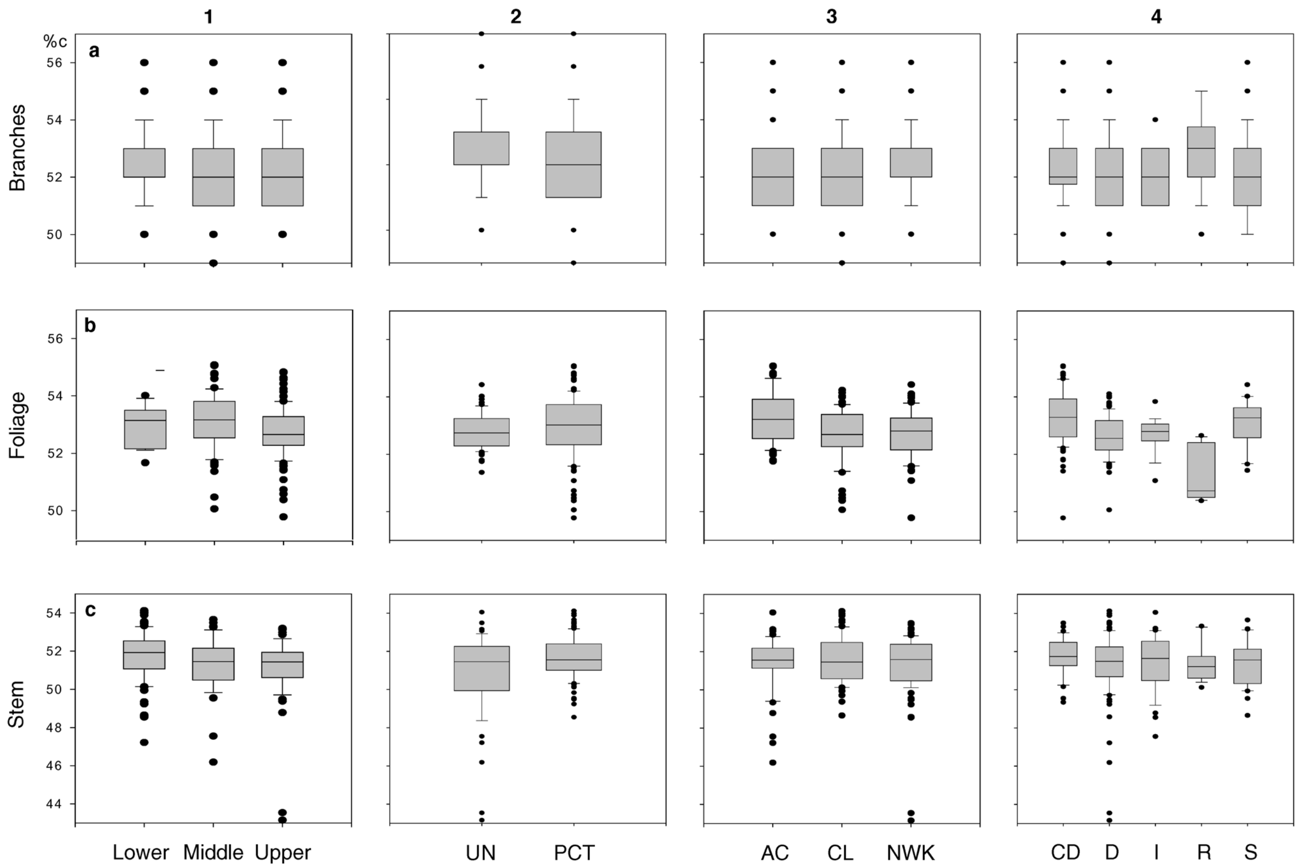

Figure 3. Effects of within-crown position (a1, b1, c1), treatment type (a2, b2, c2), study site (a3, b3, c3) and tree social class (a4, b4, c4) on percent carbon (%C by dry mass) in branches, foliage and stems of balsam fir (*Abies balsamea*). The filled circles represent outliers; the extremes of the vertical bars represent the data ranges as defined by 1.5 × inter-quartile range; the horizontal lines within the boxes represent median values; and the upper and lower bounds of the boxes represent the 2nd and 3rd quartiles, respectively. Abbreviations: UN = unmanaged; PCT = pre-commercially thinned; AC = Acadia; CL = Charlie Lake; NWK = Nashwaak Lake; CD = codominant; D = dominant; I = intermediate; R = regeneration; and S = suppressed.

Table 2. Summary of biomass and carbon content as a function of Equation 1. Abbreviations: *a*–*d* are equation coefficients determined by regression; r^2 is the coefficient of determination and provides an indication of fit between observed and predicted values; and *n* is sample number in the fitting (all $P < 0.001$).

Item	Tree part	*a*	*b*	*c*	*d*	r^2	*n*
Fresh biomass (kg)	Foliage	0.0107	–0.332	4.0327	–11.167	0.982	28
	Branches	0.0013	0.151	–1.659	4.952	0.974	28
	Crown	0.012	–0.181	2.3742	6.215	0.991	53
	Stem	0.0019	0.444	–1.679	3.244	0.969	43
	Roots	–0.0055	0.269	–0.702	0.171	0.942	12
Dry biomass (kg)	Foliage	0.0047	–0.139	1.7914	–5.089	0.962	28
	Branches	–0.0019	0.190	–2.039	5.765	0.966	28
	Crown	0.0027	0.051	–0.247	0.667	0.986	53
	Stem	0.0043	0.069	0.9097	–3.039	0.983	43
	Roots	–0.0062	0.273	–1.560	3.037	0.954	12
Carbon content (kg)	Foliage	0.0011	–0.018	0.3634	–1.176	0.966	28
	Branches	–0.0007	0.088	–0.928	2.592	0.971	28
	Crown	0.0004	0.070	–0.564	1.416	0.988	53
	Stem	0.0019	0.0494	0.315	1.182	0.984	43
	Roots	–0.0021	0.0877	–0.317	0.3094	0.960	12

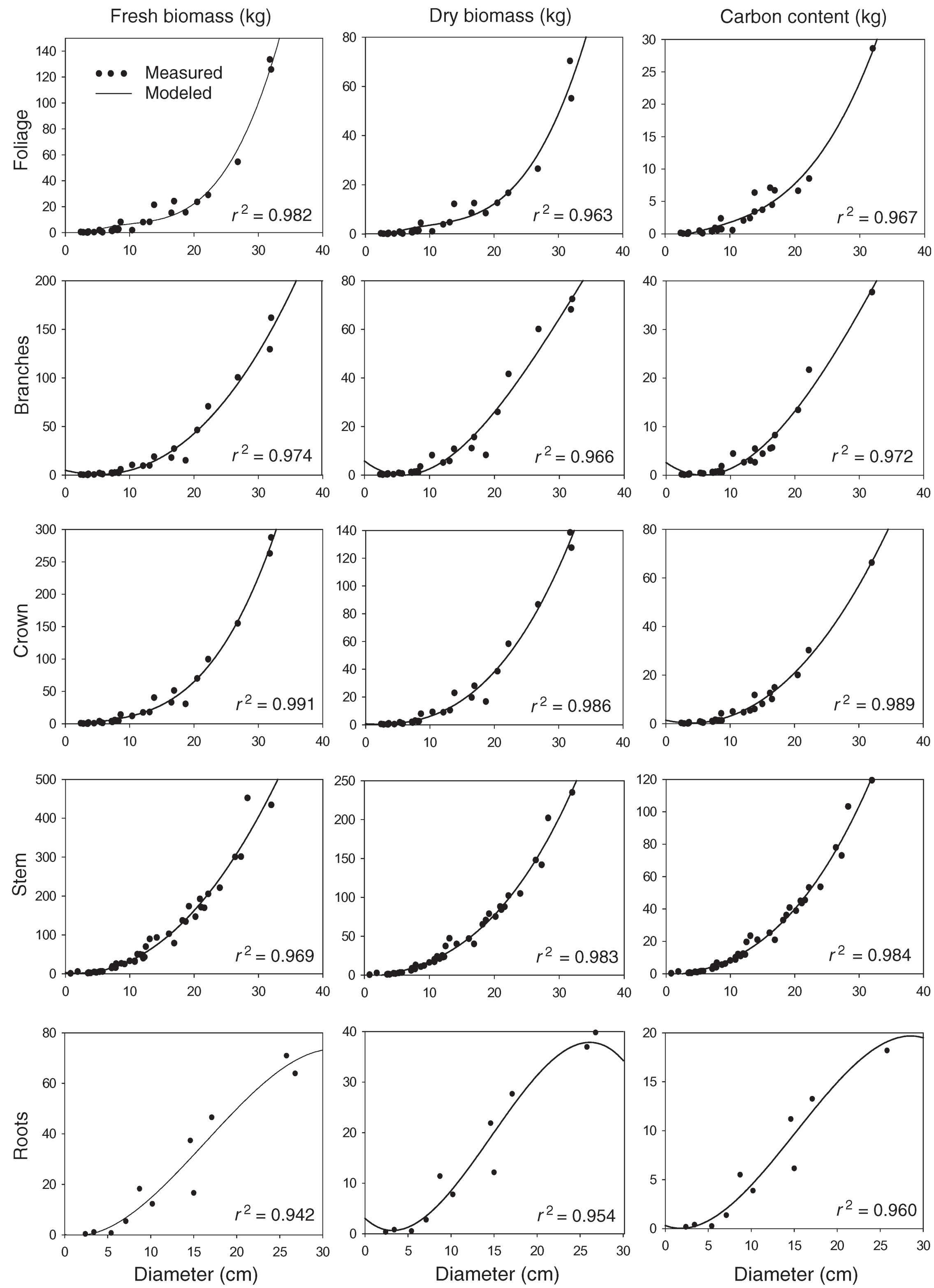

Figure 4. Comparison of observed and predicted values using a third-order polynomial (Equation 1).

ure 3a(3)) and $F_{2,\,193} = 0.76$, $P = 0.47$ for stems (Figure 3b(3)). Our results contrast with the significant differences between research sites observed in beech (Joosten et al. 2004). The large latitudinal range among the beech sites (from 6°10′ E to 9°21′ E) may account for this discrepancy. In contrast, we found that foliage %C differed by 0.65% between locations

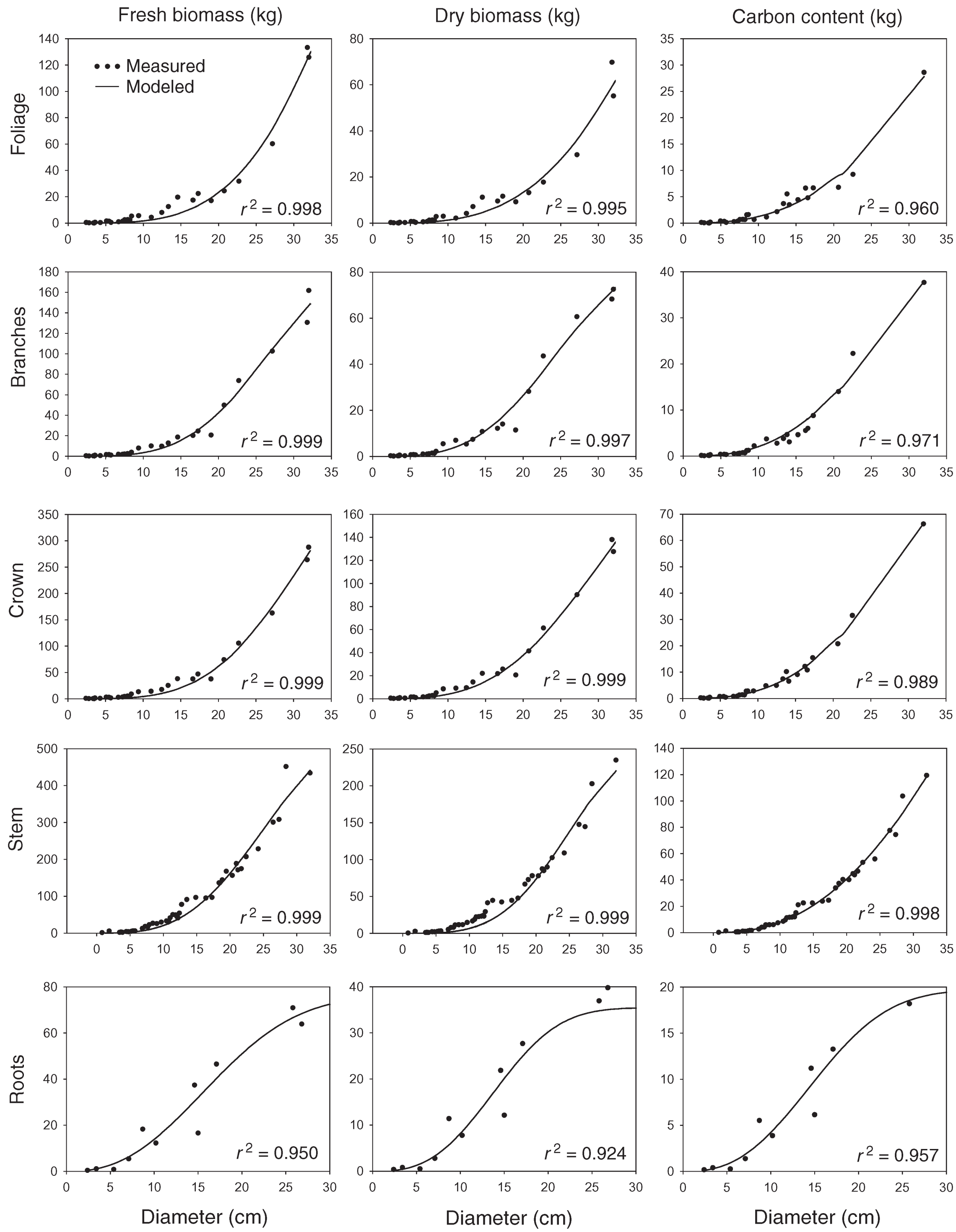

Figure 5. Comparison of observed and predicted values using a modified Weibull equation (Equation 3).

($F_{2,188} = 10.22$, $P < 0.0001$; Figure 3b(3)). This difference may be associated with the influence of environmental conditions on foliage sink–source relationships (Lacointe 2000). Grigal and Ohmann (1992) also observed differences in C storage in upland forests across five geographic zones in the Great Lake States that were related to differences in tree cover and environmental factors. Differences in C-cycling dynamics for boreal balsam fir forests across several bioclimatic regions have also been detected (Bonan 1990).

Percentage C variation among different tree social classes

There was no significant difference among the social classes of

Table 3. Summary of biomass and carbon content as a function of Equation 2. Abbreviations: *a*–*d* are equation coefficients determined by regression; r^2 is the coefficient of determination and provides an indication of fit between observed and predicted values; and *n* is sample number in the fitting (all $P < 0.001$).

Item	Tree part	*a*	*b*	*c*	*d*	r^2	*n*
Fresh biomass (kg)	Foliage	0.471	2434.38	2.7237	2.4891×10^5	0.949	28
	Branches	0.490	1726.46	2.9222	2.6352×10^5	0.974	28
	Crown	0	1203.13	3.0262	1.2708×10^5	0.992	53
	Stem	0	1.0099×10^5	2.3391	6.9266×10^5	0.968	43
Dry biomass (kg)	Foliage	0	4.0454×10^6	3.3145	6.4426×10^9	0.842	28
	Branches	0	132.374	3.3768	100890	0.971	28
	Crown	0	1031.9	2.8795	144265	0.986	53
	Stem	0	60387	2.3287	824137	0.983	43
Carbon content (kg)	Foliage	0	426882	2.6026	1.7640×10^{11}	0.962	28
	Branches	0	108.055	2.8101	32065.9	0.970	28
	Crown	0	259.9514	2.6841	32053.11	0.984	53
	Stem	0.0728	4294.777	2.3496	120168.25	0.983	43

the sampled trees in %C of branches ($F_{4, 482} = 1.01$, $P = 0.402$; Figure 3a(4)), stems ($F_{4, 191} = 0.60$, $P = 0.661$; Figure 3c(4)) and foliage ($F_{4, 186} = 11.83$, $P < 0.0001$; Figure 3b(4)). In contrast, there was a significant difference between the regeneration and suppressed social classes in foliage %C ($P = 0.0148$) and between the regeneration and codominant social classes ($P = 0.0137$).

Although there were no significant differences in %C among sites or among social classes, a small but statistically significant difference was found among within-crown positions, thinning treatment and tree components. According to Joosten et al. (2004), when a biomass-to-C content conversion factor of 50% is used in C inventories, low prediction errors of 2% at the stand level may translate to prediction errors of 10–25% at the individual tree level, which they attributed to significant regional differences in C content. When we used a conversion factor of 50% for branches and stem and 45% (based on values reported in Gower et al. 1997) for foliage, errors of 3–10% for branches and stems and 5–15% for foliage were generated at the stand level compared with the values obtained when we used our measured tree-level %C content values. These differences are substantial and indicate the need to improve existing allometric relationships for estimating tree C content, particularly when estimating forest-scale aboveground C storage based on biomass determinations by remote sensing. Although there were no measurable differences in %C in trees among different locations and social classes, the differences among treatments and within-crown positions were considerable and need to be accounted for in the biomass and C content equations. Accordingly, we derived a set of regression equations for estimating biomass and C content at the Nashwaak Lake, Charlie Lake and the Acadian Research Forest site, giving special consideration to the inherent differences in allocation differences among trees.

Growth equations of biomass and C at the tree level

Biomass is a function of tree diameter, tree height, tree location, tree age and crown position (Schroeder et al. 1997, Bond-Lamberty et al. 2002, Joosten et al. 2004). Thus, Bond-Lamberty et al. (2002) applied the following composite equation to predict aboveground biomass and coarse root biomass:

$$\log_{10} y = a + b\log_{10}\text{DBH} + c\text{Age} + d(\log_{10}\text{DBH})(\text{Age}),$$

where Age is age of the stand, DBH is stem diameter at breast height, and *a*, *b*, *c* and *d* are regression coefficients.

Forest age, however, is rarely measured with precision, whereas DBH can be measured accurately and is one of the most important independent mensurational variables employed in the prediction of tree biomass and C content (Gower et al. 1995, 1997, Zianis and Mencuccini 2003). Joosten et al. (2004) added tree height and site altitude to their prediction of C, and concluded that the most reliable equation of aboveground tree C is the power function (Joosten and Schulte 2002). According to their methods, C content is estimated from growing stock volume by applying a constant volume-to-C content conversion factor. However, estimation of growing stock volume and the application of a constant conversion factor introduce significant error in the calculation of aboveground C. Hunt et al. (1999) pointed out that net primary production (and net C increase) and growth efficiency decline in balsam fir with tree age, which underscores the difficulties associated with using a constant conversion factor.

In an attempt to find a more rigorous allometric equation, we compared three regression equations for their accuracy in predicting tree biomass and C content using DBH as the only explanatory variable. We first considered a third-order polynomial equation:

$$y = a\text{DBH}^3 + b\text{DBH}^2 + c\text{DBH} + d \quad (1)$$

where *a*, *b*, *c* and *d* are equation coefficients and *y* is either biomass (kg) or total C content (kg) for the different parts of the tree. Table 2 and Figure 4 show the parameters and correla-

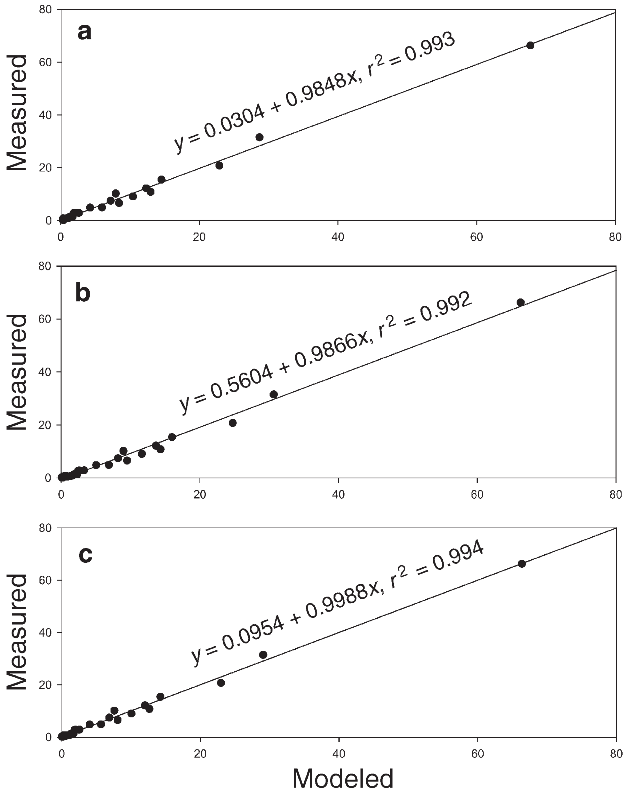

Figure 6. Comparison of observed and predicted crown % carbon content using a (a) third-order polynomial (Equation 1), (b) modified inverse polynomial (Equation 2) and (c) modified Weibull equation (Equation 3). The diagonal lines are regression lines fitted to the data.

tions for fresh biomass. We also applied the regression equation to our data set, but the r^2 values generated with this equation were generally < 0.94 and it provided poorer fits than the other equations considered. As a result, we opted not to use this regression equation for predicting tree biomass and tree C content.

The second equation considered was a modified inverse polynomial:

$$y = \frac{a + b\mathrm{DBH}^c}{\mathrm{DBH}^c + d} \qquad (2)$$

which Schroeder et al. (1997) and Joosten et al. (2004) used, except for roots. The results are shown in Table 3.

The third equation was a modified Weibull equation:

$$y = c(1 - e^{-a\mathrm{DBH}^b}) \qquad (3)$$

Of the 63 foliage samples, only 28 were used in equation derivation. The rest of the samples were removed because either the fresh foliage mass of the whole tree or the fresh branch mass of the whole tree was not measured. Results indicate that biomass and C content can be accurately predicted by DBH alone.

Equations 1 and 3 provided similar estimates of crown C content and r^2 values (0.993 and 0.994; Figure 6), slopes (0.985 and 0.999) and intercepts (0.030 and 0.095) of the lines fitted to the predicted versus observed data pairs. However, Equation 3 had the simplest form and required the fewest parameters. Equation 2 had the poorest fit, especially when applied to the root data. Figure 6 shows that Equation 2 overestimated crown C content when DBH was < 25 cm and underestimated it when DBH was > 25 cm. Thus, of the three equations assessed, Equation 3 (Table 4 and Figure 5) proved to be the most satisfactory because (1) it had the fewest equation coefficients and required the least parameterization, (2) it consistently provided a sigmoidal curve, and (3) it had the best

Table 4. Summary of biomass and carbon content as a function of Equation 3. Abbreviations: *a*–*d* are equation coefficients determined by regression; r^2 is the coefficient of determination and provides an indication of fit between observed and predicted values; and *n* is sample number in the fitting (all $P < 0.001$).

Item	Tree part	*a*	*b*	*c*	r^2	*n*
Fresh biomass (kg)	Foliage	1.13×10^{-6}	3.84	569.8	0.998	28
	Branches	2.95×10^{-5}	3.79	189.1	0.999	28
	Crown	1.10×10^{-6}	3.91	477.7	0.999	53
	Stem	2.40×10^{-5}	3.19	567.6	0.999	43
	Roots	6.84×10^{-4}	2.47	76.2	0.950	12
Dry biomass (kg)	Foliage	1.61×10^{-6}	3.41	308.8	0.995	28
	Branches	1.35×10^{-5}	3.41	86.2	0.997	28
	Crown	7.15×10^{-6}	3.39	224.7	0.999	53
	Stem	5.30×10^{-6}	3.67	260.1	0.999	43
	Roots	3.57×10^{-4}	2.86	35.5	0.924	12
Carbon content (kg)	Foliage	1.80×10^{-5}	2.79	110.8	0.960	28
	Branches	4.63×10^{-5}	2.81	68.8	0.971	28
	Crown	2.70×10^{-5}	2.91	138.7	0.989	53
	Stem	4.10×10^{-5}	2.39	798.8	0.998	43
	Roots	5.98×10^{-4}	2.60	19.7	0.957	12

overall fit (i.e., highest r^2 values, with the predicted versus observed data pairs being the closest to the 1:1 line; Figure 6c).

Based on this analysis, we consider Equation 3 to provide a good model of biomass and C partitioning in balsam fir forests in NB; the parameter values derived in this study can be used directly without major modification. To use these equations, plot-based measurements of DBH and stand density are the only inputs needed to calculate stand C.

Conclusion

Although past studies have shown that %C is uniform among different sites for particular tree species, we found significant differences in %C between the various components of a balsam fir tree. Thinning practices and crown position did not greatly affect C partitioning, and tree social class had a weak to non-existent effect on C content. Equations 1–3 all fit the data well ($r^2 > 0.90$), although Equation 2 had the least favorable fit, especially when applied to root data. Our equations enable more detailed estimates of biomass and C content of balsam fir than have hitherto been possible. Because the maximum DBH measured was 32 cm, application of our equations is limited to the narrow DBH range of 0–32 cm until an analysis has been made to determine the suitability of our equations beyond 32 cm. The derived expressions provide only an average trend description of the relationship between DBH, biomass and C content. In most cases, overestimation or underestimation at the single-tree level will be averaged out at the stand level, reducing the overall uncertainty.

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References

Barr, A., T. Griffins, A. Black, X. Lee, R. Staebler, J. Fuentes, Z. Chen and K. Morgenstern. 2002. Comparing the carbon budgets of boreal and temperate deciduous forest stands. Can. J. For. Res. 32: 813–822.

Barton, G.M. 1984. Definition of biomass samples involving wood, bark and foliage. Biomass 4:311–315.

Baskerville, G.L. 1965. Dry matter production in immature balsam fir stands. For. Sci. Monogr. 9, 42 p.

Birdsey, R.A. 1992. Carbon storage and accumulation in United States forest ecosystems. USDA For. Serv. Gen. Tech. Rep. WO–59, 51 p.

Bond-Lamberty, B., C. Wang and S.T. Gower. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Can. J. For. Res. 32:1441–1450.

Bonan, G.B. 1990. Carbon and nitrogen cycling in North American boreal forests. II. Biogeographic patterns. Can. J. For. Res. 20: 1077–1088.

Brown, S. 2002. Measuring carbon in forests: current status and future challenges. Environ. Pollut. 116:363–372.

Brown, S. and P.E. Schroeder. 1999. Spatial patterns of aboveground production and mortality of wood biomass for eastern US forests. Ecol. Appl. 9:968–980.

Brown, S., P. Schroeder and R. Birdsey. 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. For. Ecol. Manage. 96: 31–47.

Brown, S.L., P. Schroeder and J.S. Kern. 1999. Spatial distribution of biomass in forests of the eastern USA. For. Ecol. Manage. 123: 81–90.

Cannel, M.G.R. and R.C. Dewar. 1994. Carbon allocation in trees: a review of concepts for modelling. Adv. Ecol. Res. 25:59–104.

Chow, P. and G.L. Rolfe. 1989. Carbon and hydrogen contents of short-rotation biomass of five hardwood species. Wood Fiber Sci. 21:30–36.

Ecological Classification Working Group. 2003. Our landscape heritage: the story of ecological classification in New Brunswick. N.B. Dept. Nat. Resources and Energy, Fredericton, NB, Canada. CD-ROM.

Evans, J.R. 1993. Photosynthetic acclimation and nitrogen partitioning within a Lucerne canopy. II. Stability through time and comparison with a theoretical optimum. Aust. J. Plant Physiol. 20:69–82.

Freeman, B., P. Dunkier, H. Barclay, R. Morash and U. Prager. 1982. Forest biomass and nutrient studies in central Nova Scotia. Can. For. Serv., Maritimes For. Res. Cen. Inf. Rep. M-X-134, 236 p.

Good, N.M., M. Paterson, C. Brack and K. Mengersen. 2001. Estimating tree component biomass using variable probability sampling methods. J. Agric. Biol. Environ. Stat. 6:258–267.

Gower, S.T., J.G. Isebrands and D.W. Sheriff. 1995. Carbon allocation and accumulation in conifers. *In* Resource Physiology of Conifers. Eds. W.K. Smith and T.M. Hickley. Academic Press, San Diego, pp 217–254.

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik and S.J. Steele. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102:29,029–29,041.

Grigal, D.F. and L.F. Ohmann. 1992. Carbon storage in upland forests of the Lake States. Soil Sci. Am. J. 56:935–943.

Hirose, H. and M.J.A. Werger. 1987. Maximizing daily photosynthesis with respect to the leaf nitrogen pattern in the canopy. Oecologia 72:520–526.

Hollinger, D.Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. Funct. Ecol. 3:53–62.

Hollinger, D.Y., J.P. MacLaren, P.N. Beets and J. Turland. 1993. Carbon sequestration by New Zealand's plantation forests. N.Z. J. For. Sci. 23:194–208.

Hunt, Jr., E.R., M.B. Lavigne and S.F. Franklin. 1999. Factors controlling the decline of net primary production with stand age for balsam fir in Newfoundland assessed using an ecosystem simulation model. Ecol. Appl. 122:151–164.

Husch, B., T.W. Beers and J.A. Kershaw, Jr. 2003. Forest mensuration. 4th Edn. John Wiley and Sons, Hoboken, NJ, 443 p.

IPCC. 2001. Climate change. The scientific basis. Eds. J.T. Houghton, Y. Ding, M. Nogua, D. Griggs, P. Vander Linden and K. Maskell. Cambridge University Press, Cambridge, 944 p.

Ishii, H., E.D. Ford, M.E. Boscolo, A.C. Manriquez, M.E. Wilson and T.M. Hinckley. 2002. Variation in specific needle area of old-growth Douglas-fir in relation to needle age, within-crown position and epicormic shoot production. Tree Physiol. 22:31–40.

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

Jenkins, J.C., D.C. Chojnacky, L.S. Heath and R.A. Birdsey. 2004. Comprehensive database of diameter-based biomass regressions for North America tree species. USDA For. Serv. Gen. Tech. Rep. NE-319, 45 p.

Joosten, R. and A. Schulte. 2002. Possible effects of altered growth behaviour of Norway spruce (*Picea abies*) on carbon accounting. Clim. Change 55:115–129.

Joosten, R., J. Schumacher, C. Wirth and A. Schulte. 2004. Evaluating tree carbon predictions for beech (*Fagus sylvatica* L.) in western Germany. For. Ecol. Manage. 189:87–96.

Jordan, D.N. and W.K. Smith. 1993. Simulated influence of leaf geometry on sunlight interception and photosynthesis in conifer needles. Tree Physiol. 13:29–39.

Keeling, C.D., J.F.S. Chin and T.P. Whorf. 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 observations. Nature 382:146–149.

Ker, M.F. and G.D. van Raalte. 1981. Tree biomass equations for *Abies balsamea* and *Picea glauca* in northwestern New Brunswick. Can. J. For. Res. 11:13–17.

Lacointe, A. 2000. Carbon allocation among tree organs: a review of basic processes and representation in functional–structural tree models. Ann. For. Sci. 57:521–533.

Lamlom, S.H. and R.A. Savidge. 2003. A reassessment of carbon content in wood: variation within and between 41 American species. Biomass Bioenergy 25:381–388.

Lavigne, M.B. 1991. Effects of thinning on the allocation of growth and respiration in young stands of balsam fir. Can. J. For. Res. 21: 186–192.

Le Roux, X., A. Lacointe, A. Escobar-Gutiérrez and S. Le Dizes. 2001. Carbon-based models of individual tree growth: a critical appraisal. Ann. For. Sci. 58:469–506.

Liski, J., A. Pussinen, K. Pingoud, R. Makipaa and T. Karjalainen. 2001. Which rotation length is favorable to carbon sequestration? Can. J. For. Res. 31:2004–2013.

Mailard, P., E. Deleens, F. Castell and F.A. Daudet. 1999. Source–sink relationships for carbon and nitrogen during early growth of *Juglans regia* L. seedlings: analysis at two elevated CO_2 concentrations. Ann. For. Sci. 56:56–69.

Mingle, J.G. and R.W. Boubel. 1968. Proximate fuel analysis of some western wood and bark. Wood Sci. 1:29–36.

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

Reichle, D.E., B.E. Dinger, N.T. Edwards, W.F. Harris and P. Sollins. 1973. Carbon flow and storage in a forest ecosystem. *In* AEC Symposium, Carbon and the Biosphere. Eds. G.M. Woodwell and E.V. Pecan. Series No. 30, TN. Conf-720510. Tech. Information Centre, Oak Ridge, TN, pp 345–365.

Schroeder, P., S. Brown, J.M. Mo, R. Birdsey and C. Cieszewski. 1997. Biomass estimation for temperate broadleaf forests of United States using inventory data. For. Sci. 43:424–434.

Smith, W.B. and G.J. Brand. 1983. Allometric equations for 98 species of herbs, shrubs and small trees. USDA For. Serv. Res. Note NC-299, 8 p.

Ter-Mikaelian, M., and M. Korzukhin. 1997. Biomass equations for sixty-five North American tree species. For. Ecol. Manage. 97: 1–24.

Zha, T., K.-Y. Wang, A. Ryyppo and S. Kellomaki. 2002. Needle dark respiration in relation to within-crown position in Scots pine trees grown in long-term elevation of CO_2 concentration and temperature. New Phytol. 156:33–41.

Zianis, D. and M. Mencuccini. 2003. Aboveground biomass relationships for beech (*Fagus moesiaca* Cz.) trees in Vermio Mountain, Northern Greece and generalized equations for *Fagus* sp. Ann. For. Sci. 60:439–448.