Changes in organic carbon storage in a 50 year white spruce plantation chronosequence established on fallow land in Quebec¹

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Abstract: The objectives of this study were to assess the change in organic carbon (C) stocks in aboveground biomass, litter, and soil in a 50 year chronosequence of white spruce (*Picea glauca* (Moench) Voss) plantations established on non-regenerated fallow land in Quebec, and to determine the effects of ploughing (furrows) on these C stocks. Woody aboveground biomass was determined from dendrometric surveys and the use of allometric equations. The litter was sampled as well as the underlying soil in layers 10 cm thick down to 50 cm depth. The plantations under study were C sinks over the 50 year period, since they accumulated 75 Mg·ha⁻¹ during this period, with the highest rate of C accumulation occurring in the woody aboveground vegetation between 10 and 35 years. The soil at 0–30 cm depth was a C source, mainly until the plantations reached 22 years of age, with an annual loss of 0.8% over 50 years. No difference was observed among the controls and site-preparation treatments. These results suggest that 22-year-old white spruce plantations, the oldest considered for the first commitment period of the Kyoto Protocol (2008–2012), would be a small C sink (12 Mg·ha⁻¹) in southeastern Quebec but would become a larger sink for subsequent commitment periods.

Résumé : Les objectifs de l'étude consistaient à déterminer, sur une chronoséquence de 50 ans, l'évolution des stocks de carbone organique (C) dans la biomasse épigée, la litière et le sol de plantations d'épinette blanche (*Picea glauca* (Moench) Voss) établies sur des friches non régénérées au Québec et de déterminer l'effet du labourage en bandes sur ces stocks. La biomasse épigée ligneuse a été évaluée à partir d'inventaires dendrométriques et d'équations allométriques. La litière a été échantillonnée, ainsi que le sol par tranches de 10 jusqu'à 50 cm. Les plantations constituaient un puits de C pendant toute la période de 50 ans, accumulant 75 Mg·ha⁻¹ durant cette période, avec une accumulation maximale dans la biomasse épigée ligneuse entre 10 et 35 ans. Le sol (0 à 30 cm) des plantations était une source de C, surtout jusqu'à 22 ans, avec une perte annuelle de 0,8 % sur 50 ans. Aucune différence significative n'a été observée entre le traitement de préparation de terrain et les témoins. Ces résultats suggèrent que les plantations d'épinette blanche âgées de 22 ans, les plus vieilles considérées lors de la première période d'engagement au Protocole de Kyoto (2008 à 2012), seront de faibles puits de C (12 Mg·ha⁻¹) dans le sud-est du Québec mais qui deviendront plus importants lors des périodes subséquentes.

Introduction

There is general consensus within the scientific community that increasing atmospheric levels of the so-called greenhouse gases (GHGs) are causing climate change and are likely to continue to do so. GHGs arise mainly from the burning of fossil fuels, deforestation and other land-use changes, and industrial processes. The ability of forests to store and sequester atmospheric carbon dioxide (CO₂), one of the most important GHGs, is well-known and established.

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Indeed, forests represent the largest global terrestrial store of carbon (C), containing approximately 39% of global soil C and 77% of global vegetation C (Bolin et al. 2000). Terrestrial ecosystems are both sources and sinks for C. For instance, during the 1990s, terrestrial ecosystems sequestered 22% of the C released by fossil-fuel emissions. On the other hand, land-use changes during the same period (e.g., afforestation, deforestation, agriculture, and fire) were a net source of C release to the atmosphere equivalent to approximately 34% of fossil-fuel emissions (Houghton 2002). It is therefore obvious that forests and land use play an important role in the global C cycle and that gaining a clear understanding of this role is a vital component of attempts to understand and counteract the causes and consequences of climate change.

The first global attempt to deal with climate change was the United Nations Framework Convention on Climate Change (UNFCCC), which was agreed at the Earth Summit in Rio de Janeiro in 1992. By ratifying the Kyoto Agreement on 17 December 2002, Canada committed itself to bringing its annual CO_2 emissions for the period 2008–2012 down to 6% below the reference emission level of 1990. The Kyoto Protocol made provision for the use of C sequestration by forests as a means to achieve compliance with overall targets for reducing GHG emissions. There are two principal articles in the Kyoto Protocol under which countries may use forest sinks to offset GHG emissions. Article 3.3 specifies that the net contribution of emissions from sources and removals by sinks resulting from certain activities be used to meet a country's emission-reduction commitment. Sources and sinks are limited to those "resulting from direct humaninduced land-use change and forestry activities limited to afforestation, reforestation, and deforestation since 1990" (Intergovernmental Panel on Climate Change 2000). According to the terminology of the Kyoto Protocol, afforestation is tree planting on land that has not been forested for at least 50 years, while reforestation is tree planting on land that was forested but was converted to nonforested land before 31 December 1989. In this study, both afforestation and reforestation are referred to as afforestation. Article 3.4 refers to additional human-induced activities in the agriculture, land use change, and forestry sectors, again which have taken place since 1990, but in the case of forests applies only to those that were in existence prior to 1990, to avoid double accounting. Forest management is one of the eligible activities under Article 3.4, but its use, during the first commitment period, as a potential means to improve forest C sequestration is still under examination by Canada. So forest areas that will definitely be taken into account for the first commitment period will be plantations established on nonregenerated fallow land (<30% canopy projection) and ranging from 1 to 22 years of age. Sixty-seven percent of afforestation on private land in Canada between 1990 and 2002 occurred in Quebec (White and Kurz 2005) and most of it was done with white spruce (Picea glauca (Moench) Voss; Parent 2003; Thiffault et al. 2003). Thus, an important proportion of the forest accounted for during the first commitment period of the Kyoto Protocol will consist of white spruce plantations established in Quebec on non-regenerated fallow land since 1990. Taking young plantations into account is important, since Canada's natural forests will probably be a source of C for the atmosphere in 2008–2012, since they have already been identified as a source of CO₂ in the 1990s (Kurz and Apps 1999).

A change in land use from agriculture to forestry implies that the annual cycle of cultivating and harvesting crops is replaced by the much longer forest harvest cycle. This enables the development of a larger biomass and reduces soil disturbance. Forests store C in aboveground biomass, belowground biomass, soil, and litter (i.e., forest floor and coarse woody debris). For example, in a study conducted in 18-year-old lobolly pine (Pinus taeda L.) plantations in Tennessee, Johnson et al. (2003) showed that in less than 20 years, the ecosystem C content had tripled, primarily because of increases in tree biomass. Soil C accumulation in plantations following afforestation is highly variable, depending mainly on the depth of sampling and the chronosequence studied (Polglase et al. 2000). Those authors, reporting results from 197 sites from around the world, estimated that in a majority of these studies, changes in soil C content are estimated to be around $\pm 2.5\%$ per year (or $\pm 1.5 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$). Mineral-soil C content generally decreases during the first 10 years following afforestation, particularly during the first 5 years; this is followed by a recovery, slow at the beginning but faster as the stand matures. This first period of soil C decrease can vary from 3 to 35 years following afforestation of fallow land (Zak et al. 1990; Richter et al. 1999). This is due to the fact that in young plantations, C losses through soil respiration are greater than C inputs to soil via litterfall, and the low litterfall is due to the low production of dead biomass. The equilibrium between litterfall and forest-floor decomposition is reached at different ages depending on plantation characteristics (Wilde 1964; Compton et al. 1998).

It is necessary to document the C budget for afforested fallow land (previously cultivated soils) in Quebec to verify the real state (sink or source) of these plantations and estimate the evolution of C storage in such ecosystems over time. The objectives of this study were to assess the temporal changes in C stocks in aboveground biomass, litter, and soil (0–30 cm depth) in white spruce plantations established on non-regenerated fallow land in the Bas Saint-Laurent region of Quebec and determine the effect of ploughing (furrows 2 m apart) on these C stocks. Two hypotheses concerning soils were tested: (1) for plantations aged 0–20 years, the soil is a C source, and (2) ploughing causes a more significant loss of soil C during the first years after afforestation.

Material and methods

Study area

The study area is located in the southeastern part of the province of Quebec in the Great Lakes - St. Lawrence Forest Region as delineated by Rowe (1972). It corresponds to ecoregions 4fT, 4fM, and 4gT (Saucier et al. 1998), which belong to the eastern balsam fir (Abies balsamea (L.) Mill.) yellow birch (Betula alleghaniensis Britton) bioclimatic subdomain (Fig. 1). The climatic and growth conditions in this subdomain are as follows: 1250-1450 degree-days above 5 °C, growing-season precipitation 250-300 mm, growing-season cumulative vapour pressure deficit 1050-1350 mbar (1 mbar = 0.1 kPa), mean annual temperature 1-3 °C, and annual precipitation 1000-1200 mm. These values were extracted from climate maps compiled by Noël (2002), with long-term averages (1961–1990) obtained from Ung et al. (2001) and the BioSim program (Régnière et al. 1995). The growing season lasts from 150 to 160 days (Robitaille and Saucier 1996). The topography is moderately rolling with altitudes ranging from 275 to 575 m. The parent material originates from sedimentary rocks, shales, sandstone, conglomerates, and volcanites. The most common landform features originate from glacial activity and include ground and end moraines of various thicknesses and residual material resulting from bedrock weathering. Bedrock outcrops are present but cover small areas. Soils are generally deep, well-drained loam to sandy loam, classified as orthic humo-ferric Podzols (Soil Classification Working Group 1998) or Haplorthods (Soil Survey Staff 1988).

The chronosequence approach

Plantations were selected to be as comparable as possible, except in age. Besides being on non-regenerated fallow land larger than 1 ha in area, they had to have soils that were Fig. 1. Location of plantation in the Bas Saint-Laurent region, Quebec.



alike with regard to soil order (Podzols), water regime (mesic), and soil texture (sandy to sandy loam). However, type of crops previously grown remained unknown in most cases. The chronosequence studied was composed of 57 plantations distributed among seven different ages: ten 0-, ten 2-, fourteen 5-, ten 10-, five 22-, four 35-, and four 50-year-old plantations. Age 0 corresponds to the year of planting. The 35 year age class includes 34- to 37-year-old plantations, while the 50 year class includes 45- to 55-year-old plantations. The close ages at the beginning of the chronosequence (0, 2, and 5 years) were selected to verify the hypothesized short-term soil C decrease following afforestation, particularly in the case of site preparation. For the four youngest plantation ages, half of the sites were ploughed (furrows 2 m apart) before being planted, while the other half were not disturbed by preparatory ploughing (control plots). For the three oldest plantations, it was impossible to know whether or not the sites had been prepared before planting. Thus, the replication at each age and site-preparation level was five to nine plantations for ages 0, 2, 5, and 10 years, but four or five plantations for ages 22, 35, and 50 years with no site preparation. This number of replicates was chosen to reduce variability in C content from sources other than plantation age and site-preparation level, such as spatial variability. Also, for reducing variability in soil C content, an area of non-afforested fallow land was selected in the neighbourhood of each plantation and the first 20 cm of soil was sampled. This paired sample was used to underscore the afforestation effect on soil C content. All the sites were planted with 4-year-old bare-root seedlings and plantations were never thinned. Planting density of the 0- to 22-year-old plantations was 2500 seedlings per hectare, while the density of the 30- and 50-year-old plantations ranged from 2217 to 2917 seedlings per hectare, except for one plantation (5650 seedlings per hectare). The planted species was white spruce, alone or mixed with Norway spruce (Picea abies (L.) Karst), black spruce (Picea mariana (Mill.) BSP), white pine (Pinus strobus L.), red pine (Pinus resinosa Ait.), or tamarack (Larix laricina (Du Roi) K. Koch). In mixed stands, white spruce was always the dominant species (more than 75% of total density). All the measurements were made during summer 2004.

Dendrometric measurements

One plot was established per plantation. The plot location was chosen to be representative of the plantation-selection criteria. The area considered and dendrometric variables measured depended on the age of the plantation and the status of the woody vegetation (planted or not planted; Table 1). An electronic vernier scale was used to measure diameter at stump height (mm), whereas diameter at breast height (cm) was measured with a calliper. Height was measured with a ruler (cm; trees less than 3 m in height) or a vertex hypsometer (m; trees more than 3 m in height).

Litter and soil sampling

Herbaceous plants, dead or alive, and the L and F horizons of the forest floor were sampled with a punch (177 cm^2) at four random locations within each 400 m² plot. Samples were stored in paper bags until their arrival at the laboratory.

Two pits were dug, randomly positioned along a diagonal of the 400 m² plot. In each pit, soil samples were taken at every 10 cm depth down to 50 cm. For each layer, three soil samples were taken: two volumetric samples (200 cm³ each) and one bulk sample. The H layer of the forest floor was included in the 0–10 cm sample when it was present. In the neighbouring area, on non-afforested fallow land, soils were sampled down to 20 cm with a bucket auger in three locations, after removal of the L and F parts of the organic layer. These three soil samples were composited before being analysed.

Laboratory analyses

Litter and soil samples were stored in a freezer upon arrival at the laboratory until they could be processed. Prior to analysis, litter samples were oven-dried (65 °C, ≥48 h) before being weighed and ground. Soils of the volumetric cores were air-dried (\geq 48 h) and sieved through 2 mm mesh. Bulk density was determined as described by Federer et al. (1993). After measurement of bulk density, subsamples of sieved soils were ground with mortar and pestle. Total C content was determined by dry combustion with a LECO CR-412 carbon analyser on all ground subsamples. Total C content was based on oven-dried mass. Total C content was presumed to equal organic C content, since sampled soils were acid Podzols; we avoided calcareous soils in the region, which are found only in some poorly drained depressions (e.g., Chabot soil series) and on clay deposits (e.g., Kamouraska soil series; Baril and Rochefort 1979).

Estimation of total C content

For each plantation, organic C content was estimated in three compartments of the ecosystem: soil, litter, and aboveground woody vegetation. Calculation of C stocks in the soil and litter is described in Tremblay et al. (2002). Aboveground woody vegetation biomass (anhydrous) of each tree or shrub in each plot was computed using allometric equations from the scientific literature. To predict biomass, five different equations were used, depending on plant species (Appendix A). All equations used diameter to predict biomass: diameter at stump height (DSH), diameter at 15 cm (D15), or diameter at breast height (DBH). Diameter at 15 cm was never measured, so it was estimated using the

Table 1. Dentrometric variables measured according to the age of the plantation.

	Aged 0-5 years	Aged 10-50 years
Planted vegetation	Diameter at stump height for all planted trees in the 400 m^2 plot	Diameter at breast height for all planted trees in the 400 m ² plot
	Height of all planted trees in the 400 m ² plot	Height of 15 trees, including 8 dominants; these trees were randomly chosen but were located in the 400 m ² plot
Unplanted vegetation	Diameter at breast height or diameter at stump height when diameter at breast height was not measurable; this was measured in a 127 m ² subplot	Diameter at breast height or diameter at stump height when diameter at breast height was not measurable; this was measured in a 40 m ² subplot

following equation (parameter values a_{15} and b_{15} are indicated in Appendix A).

[1]
$$D15 = \frac{DSH - a_{15}}{b_{15}}$$

Biomass computed for each individual tree or shrub was converted to C content using conversion factors of 0.49 for deciduous species and 0.50 for coniferous species (Matthews 1993).

Statistical analyses

Two kinds of analysis of variance were performed in this study. In the first case, a three-way repeated-measurement analysis of variance was used to determine whether mean C content of a given compartment (soil, litter, or aboveground woody vegetation) varied among plantation ages (0, 2, 5, 10, 22, 35, and 50 years) and site-preparation treatment. In this paper, only 0-10 and 0-30 cm soil layers were tested. Plantation location was used as the random level, whereas site preparation, plantation age, and the compartments were defined as fixed effects, as well as all interactions between these three factors. In this analysis, compartments were used as levels of a repeated factor. Several covariance structures were tested. The choice of the best structure of covariance was based both on Akaike's information criterion and on the likelihood ratio test between covariance structures taken two by two. In the second case, a two-way analysis of variance was used to determine if the total C content of a plantation was related to its age plantation and to site preparation. Plantation location was used as a random effect, whereas site preparation and plantation age were defined as fixed effects, as well as the interaction between these two factors. In both analyses, the soil C content at 0-20 cm depth in an adjacent piece of fallow land was used as a potential covariable. Because this covariable and the "sitepreparation" effect were never significant, and because of the presence of empty cells (there were no ploughed plantations aged 22, 35, or and 50 years), we chose to redo the statistical analyses without these two variables.

Since there was no significant correlation (p > 0.05) between the C content of the aboveground woody vegetation, litter, and soil, we used the variance component structure. We used Helmert's contrasts to determine the age of the plantation at which the C content ceased to change. Naturallog transformation was necessary to fulfil the requirements regarding normally distributed errors and homogeneity of variances. Means and their approximate confidence limits (95%) were computed on the logarithmic scale and then back-transformed using the method proposed by Végiard and Ung (1993) to reduce the bias introduced by the transformation. All tests were conducted with a probability of type I error of $\alpha = 5\%$. All statistical analyses were carried out using the MIXED procedure in SAS[®] (SAS Institute Inc. 2003).

The C-accumulation rate (%) between two age classes was calculated with natural-log values, using the following formula

[2]
$$\Delta Y = 100(e^{\text{diff.}} - 1)$$

where ΔY is the difference between two C contents (%) and "diff." is the difference between two C contents (natural log).

Even though the data come from selected plantations with characteristics of interest rather than from a controlled experimental design with randomization, we use "effect", "treatment", and "control" in their broader sense, to make it easier to interpret the statistical results.

Results

The C content of the pools varied significantly as a function of plantation age, but the differences depended on the pool type (p < 0.001; Table 2). The mean C content of the aboveground woody vegetation increased from 1 to 97 Mg·ha⁻¹ from ages 0 to 35 years (Fig. 2), and stabilized from age 35 years onward (Table 2). The C content at age 22 years was only half of that observed at age 50 years. The highest increase occurred between ages 10 and 35 years, with sequestration of 93 Mg C·ha⁻¹, corresponding to accumulation of 6.2 Mg C·ha⁻¹·year⁻¹. The mean net sequestration rate in the aboveground woody vegetation was 1.9 Mg C·ha⁻¹·year⁻¹ during the 50 years.

The mean litter C content increased from 5 to 9 Mg·ha⁻¹ between ages 0 and 35 years (Fig. 2), and stabilized from age 35 years onward (Table 2). Litter C sequestration was negligible until age 22 years, but maximal between ages 22 and 35 years, with accumulation of 4 Mg·ha⁻¹, or relative accumulation of 70% (CI = 18%-145%). This corresponds to accumulation of 0.3 Mg C·ha⁻¹·year⁻¹ between ages 22 and 35 years. The mean net C sequestration rate in the litter was 0.06 Mg·ha⁻¹·year⁻¹ during the 50 years, and nil during the first 22 years.

The mean C content of the 0–30 cm soil layer decreased from 74 to 47 Mg·ha⁻¹ between ages 0 and 22 years (Fig. 2), and stabilized from age 22 years onward (Table 2). The

Table 2. Sources of variation, associated degrees of freedom of the numerator and the denominator, F values, and associated p values for carbon (C) content by compartment.

Source of variation (fixed effects)	Numerator df	Denominator df	F	p > F
Age	6	77.9	101.16	< 0.0001
Compartment	2	71.2	880.37	< 0.0001
Age × compartment	12	84.6	110.10	< 0.0001
0-30 cm soil layer				
0 years vs. other ages	1	149	3.96	0.0481
2 years vs. other ages	1	147	4.37	0.0386
5 years vs. other ages	1	123	16.65	< 0.0001
10 years vs. other ages	1	106	5.15	0.0251
22 years vs. other ages	1	85.2	0.42	0.5188
35 vs. 50 years	1	17	0.06	0.8073
Litter				
0 years vs. other ages	1	149	2.46	0.1190
2 years vs. other ages	1	149	6.35	0.0130
5 years vs. other ages	1	131	1.30	0.2574
10 years vs. other ages	1	116	10.43	0.0016
22 years vs. other ages	1	95.2	10.11	0.0020
35 vs. 50 years	1	17	0.04	0.8495
Aboveground woody vegetation				
0 years vs. other ages	1	149	522.12	< 0.0001
2 years vs. other ages	1	149	688.54	< 0.0001
5 years vs. other ages	1	131	1001.09	< 0.0001
10 years vs. other ages	1	116	617.52	< 0.0001
22 years vs. other ages	1	95.2	27.35	< 0.0001
35 vs. 50 years	1	17	0.02	0.8910

Fig. 2. Carbon (C) contents of the three compartments in a chronosequence of white spruce plantations. The solid symbols represent means that are significantly different from succeeding means (p < 0.05) and the open symbols those that are not significantly different from succeeding means. Analyses were performed on natural-log-transformed data. The figure shows adjusted back-transformed means (Mg C·ha⁻¹) with their 95% confidence intervals. Means were linked using a spline interpolation method to illustrate the evolution of C stocks. The vertical line indicates the age of the oldest plantations for the first commitment period of the Kyoto Protocol (22 years).



highest loss occurred between ages 10 and 22 years, with a loss of 20 Mg C·ha⁻¹ (42%, CI = 4%–95%) or a loss of 1.6 Mg C·ha⁻¹·year⁻¹ (3.5%) during this period. The loss over 50 years was 22 Mg C·ha⁻¹, corresponding to a relative loss of 0.8% annually. The mean loss in the 0–30 cm layer was 0.4 Mg C·ha⁻¹·year⁻¹ over 50 years and 1.3 Mg C·ha⁻¹·year⁻¹ during the first 22 years. The mean C content of the 0–10 cm soil layer varied in the same manner as that of the 0–30 cm layer (data not shown).

The total C content of the plantations, taking the whole 30 cm soil depth into consideration, increased from 79 to 142 Mg·ha⁻¹ between ages 0 and 35 years (Fig. 3) and stabilized from age 35 years onward (Table 3). The total C content at age 50 years was 1.7 times the content at age 22 years. The mean net sequestration rate over 50 years was 75 Mg C·ha⁻¹ (1.5 Mg C·ha⁻¹·year⁻¹) or 275 Mg CO₂·ha⁻¹ (5.5 Mg CO₂·ha⁻¹·year⁻¹), corresponding to an increase of 2.0% annually during this period. During the first 22 years, the mean net sequestration rate was 12 Mg C·ha⁻¹ (0.6 Mg C·ha⁻¹·year⁻¹) or 44 Mg CO₂·ha⁻¹ (2 Mg CO₂·ha⁻¹·year⁻¹).

At the time of afforestation, the 0–30 cm soil layer was the largest pool (74 Mg C·ha⁻¹), followed by the litter (5 Mg C·ha⁻¹) and aboveground woody vegetation (1 Mg C·ha⁻¹) (Fig. 4). Ten years later, there was as much C in the aboveground woody vegetation as in the litter (4–5 Mg·ha⁻¹). At age 22 years, there was as much C in the aboveground woody vegetation as in the 0–30 cm soil layer (41– 50 Mg·ha⁻¹). Finally, at age 50 years, there was almost twice as much C in the aboveground woody vegetation (94 Mg·ha⁻¹) as in the 0–30 cm soil layer (53 Mg·ha⁻¹).

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Source of variation (fixed effects)	Numerator df	Denominator df	F	p > F
Age	6	26.6	9.04	< 0.0001
0 years vs. other ages	1	48.5	5.83	0.0196
2 years vs. other ages	1	19.4	9.73	0.0030
5 years vs. other ages	1	49.4	6.03	0.0177
10 years vs. other ages	1	47.4	24.46	< 0.0001
22 years vs. other ages	1	43	11.25	0.0017
35 vs. 50 years	1	6	0.33	0.5886

Table 3. Sources of variation, associated degrees of freedom of the numerator and denominator, F values, and associated p values for total ecosystem C content.

Fig. 3. Total C contents in a chronosequence of white spruce plantations. The solid symbols represent means that are significantly different from succeeding means (p < 0.05) and the open symbols those that are not significantly different from succeeding means. Analyses were performed on natural-log-transformed data. The figure shows back-transformed adjusted means (Mg C·ha⁻¹) with their 95% confidence intervals. The means were linked using a spline interpolation method to illustrate the evolution of C stocks. The vertical line indicates the age of the oldest plantations for the first commitment period of the Kyoto Protocol (22 years).



Discussion

The results obtained in this study did not confirm the hypothesis that ploughing leads to more soil C loss during the first years following afforestation. Paul et al. (2002) reported the same result from a compilation of 204 studies for a 10 year chronosequence after plantation. Our results rather suggest that a decrease in soil C content during the first years after plantation establishment, in ploughed plantations or controls, would be caused by low soil C inputs from litterfall, owing to slow vegetation growth during this period. Also, the fact that ploughing was done on only a small proportion of the plantation area, could explain the absence of a difference between ploughed plantations and controls.

The aboveground woody vegetation was the compartment in which most of the sequestration had occurred over 50 years. This result is in accordance with the finding of Schiffman and Johnson (1989) that most of the C sequestered during 50 years after plantation establishment was in tree biomass. However, the relative importance of the C content in the aboveground woody vegetation and soil could Fig. 4. Partitioning of total ecosystem C content in a chronosequence of white spruce plantations.



vary with soil type (Thorn et al. 1997). On poorer soils, C sequestration could be slower in vegetation and faster in the soil, owing to a lower growth rate of the vegetation and a lower decomposition rate of the organic matter. The mean aboveground biomass at ages 35 and 50 years was in the same range as that calculated with volumes derived from recent surveys in the same plantations, using white spruce wood density of 0.386 Mg organic matter m⁻³ (Berry 1987) and a conversion factor of 1.454 (Harding and Grigal 1985) to convert stem volume without bark to stem volume including bark and branches. However, the plateau observed between ages 35 and 50 years (Fig. 2) was unexpected, since white spruce should still grow after age 35 years. Berry (1987) found that for most spacing and site index classes, the mean annual increment for total biomass of white spruce in plantations reaches a maximum between ages 50 and 55 years. The mean C stock of the aboveground woody vegetation of the 50-year-old plantations in our study was lower than stocks generally observed in white spruce plantations with the same site index value (Berry 1987). Our result may be explained by the fact that one of the four 50-year-old plantations exhibited a high mortality rate (40%) because of spruce budworm infestation, while another had a high plantation density (5650 stems \cdot ha⁻¹).

The litter C content increased mainly between ages 22 and 35, and stabilized between ages 35 and 50. The lag period of 22 years before litter accumulated, and the plateau at 35 years, are difficult to interpret, since litter C content results from the growth and decline of herbaceous plants dur-

ing canopy closure (between 10 and 22 years) and L-F layer accumulation. Vesterdal et al. (2002) and Richter et al. (1999) reported higher C sequestration, in forest floor only, for Norway spruce (9 Mg·ha⁻¹ over 29 years) and lobolly pine (37.8 Mg·ha⁻¹ over 40 years) plantations in Denmark and South Carolina, respectively. In the present study, only 3.2 Mg C·ha⁻¹ was sequestered in the litter over 50 years. This could be partly due to a lower growth rate for white spruce, and thus a lower litterfall rate, under our less favourable growth conditions (a growing season of 150–160 days). Vesterdal et al. (2002) reported that litterfall offset the decrease in mineral-soil C, while Richter et al. (1999) reported that litter made the soil compartment a net C sink. However, in this study, litter input did not appear to counteract the decrease in soil C.

The hypothesis that soil is a mid-term C source following afforestation was confirmed in this study. The soil compartment showed a C decrease in the 0-10 and 0-30 cm soil layers, mainly during the first 22 years following afforestation, with or without ploughing. The soil C content ceased to decrease between plantation ages 22 and 50 and remained stable at around 23 Mg·ha⁻¹ for the 0-10 cm layer and 50 Mg·ha⁻¹ for the 0–30 cm layer. This decrease is in opposition to the results obtained by Bouwman and Leemans (1995) but in accordance with those of Paul et al. (2002), Vesterdal et al. (2002), and Richter et al. (1999). The mean annual net rate of decrease over 50 years (-0.8% for the 0-30 cm layer) is in the same range as the rates reported in the worldwide compilation of 197 plantations $(\pm 2.5\%)$ by Polglase et al. (2000). However, this rate of decrease is opposite to the mean rate of increase reported for plantations older than 30 years (+0.4%) by Paul et al. (2002). The mean rate of decrease for the 0-30 cm soil layer between ages 0 and 50 years (-40%, CI = -0.2% to -95%) is higher than the rate reported for 65 resinous plantations (-12%) by Guo and Gifford (2002). The C decrease in the 0-10 and 0-30 cm mineral-soil layers may be explained by a litterfall rate lower than the decomposition rate of the organic matter, especially in young plantations.

It is possible that we underestimated the soil C content in the superficial mineral-soil layers because of decreasing soil density over time (Ellert et al. 2002), leading to overestimation of the decrease in soil C. To take this bias into account and measure the evolution of the C content of a fixed "pure" mineral-soil mass rather than a fixed soil volume, the thickness of a given soil layer should be adjusted with changing density. Sample calculations show that correcting soil-layer values for a fixed mineral-soil mass would cause soil C stocks in the first 30 cm of pure mineral soil to increase by up to 10%. Correcting for changes in bulk density would not, however, change the overall result: a decrease in soil C content during the first 50 years following afforestation with white spruce.

Total plantation C storage was underestimated in this study, since root C content was not measured. In the compilation by Jenkins et al. (2003), the root biomass : above-ground biomass ratio was constant during the entire tree life and was estimated at around 25% for spruces. Taking coarse roots into account, using this ratio would increase plantation C sequestration by 23 Mg·ha⁻¹ in 50 years and by 10 Mg·ha⁻¹ in 22 years, or 0.5 Mg·ha⁻¹ year⁻¹ for both periods.

In the 22-year-old plantations, the oldest ones considered for the first commitment period of the Kyoto Protocol, trees were in an active phase of growth, sequestering C in their biomass, but soil was losing C, leading to low overall C sequestration (12 Mg·ha⁻¹ considering the first 30 cm soil layer). However, we expect that the afforestation that has taken place since 1990 will be more useful in compensating for GHG emissions for subsequent commitment periods (75 Mg C·ha⁻¹ sequestered in 50-year-old plantations). Despite the results indicating that soil is not a C sink during the 50 years after planting, it remains an important C pool, playing a key role in the global C cycle after nonforested land is converted to forested land. Soil C is more resistant than C sequestered in the vegetation to changes produced as a result of forest management (Johnson and Curtis 2001). C in forest products may be rapidly released into the atmosphere, whereas soil C content is more stable over time. The quality of sequestered soil C should be studied with respect to its resistance to disturbances.

Taking the three compartments into account, white spruce plantations acted as a small C sink over 22 years and an important C sink over 50 years in the eastern balsam fir – yellow birch subdomain. The estimated net sequestration rate is, however, imprecise because of the large confidence intervals of the back-transformed adjusted means for aboveground woody vegetation at 35 years (72-129 Mg C·ha⁻¹) and 50 years (70–125 Mg C·ha⁻¹). Vesterdal et al. (2002) reported a sequestration rate of 100 Mg C·ha⁻¹ or 365 Mg $CO_2 \cdot ha^{-1}$ for 28- to 29-year-old *Picea abies* plantations. This sequestration rate is 37% higher than that estimated in this study at a plantation age of 35 years (63 Mg C·ha⁻¹ or 230 Mg CO₂·ha⁻¹), probably because of the different tree species and more favourable growth conditions in Denmark (mean annual temperature 7.7 °C and mean annual precipitation 600 mm) than in the bioclimatic subdomain in the present study (mean annual temperature 1-3 °C and mean annual precipitation 1000–1200 mm).

The next step in our study will be to compare C sequestration in non-afforested fallow land with that in afforested land to estimate the net sequestration rate caused by afforestation. This information is required by the Kyoto Protocol to determine the net impact of afforestation of non-regenerated fallow land on C sequestration. Moreover, C sequestration in white spruce plantations should be documented for more acid soils such as those in the Laurentian and Canadian Shield regions. The podzolization process in these more acid soils should further increase soil C sequestration because of the higher concentration of dissolved organic C in percolating water.

Conclusion and recommendations

Afforestation of non-regenerated fallow land with white spruce, with or without ploughing (furrows 2 m apart), in the eastern balsam fir – yellow birch subdomain led to mean total net sequestration of 75 Mg $C\cdot$ ha⁻¹ or 275 Mg $CO_2\cdot$ ha⁻¹ over 50 years, corresponding to a mean rate of 1.5 Mg $C\cdot$ ha⁻¹ vyear⁻¹ or 5.5 Mg $CO_2\cdot$ ha⁻¹ vyear⁻¹. These amounts would have been higher if roots and calculations for a fixed soil mass had been taken into account. The highest net C sequestration rate occurred in aboveground

The 22-year-old plantations, the oldest ones taken into account for the first commitment period of the Kyoto Protocol, are a small C sink (+0.5 Mg C·ha⁻¹·year⁻¹), since the aboveground woody vegetation was a sink (+1.8 Mg C·ha⁻¹·year⁻¹), the litter was neutral (remained stable), and the 0–30 cm soil layer was a source (-1.3 Mg C·ha⁻¹·year⁻¹).

Although soil did not act as a C sink in the 50 year chronosequence studied, it remains a key compartment in the global C cycle, as a more important and stable C pool than vegetation when nonforested land is converted to forested land. Studies emphasizing soil C sequestration and the factors that influence it (e.g., climate, agricultural practices prior to planting, soil texture, species used for afforestation) are needed to ensure that this long-term CO_2 sink is maximized.

We recommend pursuing the following avenues of research: (*i*) adding the root compartment to the C-budget analysis, (*ii*) studying chronosequences of nonforested fallow land to verify whether or not their C contents are higher than those in afforested land at a given age, (*iii*) adding older plantations on fallow land to the chronosequence to verify when the soil becomes a C sink, and (*iv*) establishing a chronosequence of fallow land and white spruce plantations on more acid soils, such as those found on the Canadian Shield. These studies would provide reliable information to decision makers, who would then know where and which species to plant, to maximize CO₂ sinks to meet Kyoto Protocol requirements.

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References

- Baril, R., and Rochefort, B. 1979. Étude pédologique du comté de Rivière-du-Loup. Direction de la recherche, Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec, Québec, Que.
- Berry, A.B. 1987. Plantation white spruce variable density volume and biomass yield tables to age 60 at the Petawawa National Forestry Institute. Can. For. Serv. Inf. Rep. PI-X-71.
- Bolin, B., Sukumar, R., Ciais, P., Cramer, W., Jarvis, P., Kheshgi, H., Nobre, C., Semonov, S., and Steffen, W. 2000. Global perspective. *In* Land use, land-use change, and forestry. *Edited by* R.T. Watson, I.R. Noble, B. Bolin, N.H. Ravindranath, D.J. Verardo, and D.J. Dokken. Cambridge University Press, Cambridge. pp. 23–52.
- Bouwman, A.F., and Leemans, R. 1995. The role of forest soils in the global carbon cycle. *In* Carbon forms and function in forest soils. *Edited by* W.F. McFee and F.M. Kelly. Soil Science Society of America, Inc., Madison, Wis. pp. 503–525.
- Compton, J.E., Boone, R.D., Motzkin, G., and Foster, D.R. 1998. Soil carbon and nitrogen in a pine–oak sand plain in central Massachusetts: role of vegetation and land-use history. Oecologia, 116: 536–542.
- Ellert, B.H., Janzen, H.H., and Entz, T. 2002. Assessment of a method to measure temporal change in soil carbon storage. Soil Sci. Soc. Am. J. 66: 1687–1695.
- Federer, C.A., Turcotte, D.E., and Smith, C.T. 1993. The organic fraction – bulk density relationship and the expression of nutrient content in forest soils. Can. J. For. Res. 23: 1026–1032.
- Guo, L.B., and Gifford, R.M. 2002. Soil carbon stocks and land use change: a meta analysis. Global Change Biol. 8: 345–360.
- Harding, R.B., and Grigal, D.F. 1985. Individual tree biomass estimation equations for plantation-grown white spruce in northern Minnesota. Can. J. For. Res. 15: 739–739.
- Houghton, R.A. 2002. Magnitude, distribution and causes of terrestrial carbon sinks and some implications for policy. Clim. Policy, 2: 71–88.
- Intergovernmental Panel on Climate Change. 2000. Land use, landuse change, and forestry. Cambridge University Press, Cambridge.
- 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: 12–35.
- Johnson, D.W., and Curtis, P.S. 2001. Effects of forest management on soil C and N storage: meta-analysis. For. Ecol. Manage. 140: 227–238.
- Johnson, D.W., Todd, D.E., Jr., and Tolbert, V.R. 2003. Changes in ecosystem carbon and nitrogen in a loblolly pine plantation over the first 18 years. Soil Sci. Soc. Am. J. **67**: 1594–1601.
- Kurz, W.A., and Apps, M.J. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Appl. 9: 526–547.
- Matthews, G. 1993. The carbon content of trees. For. Comm. Tech. Pap. 4, Edinburgh, UK.
- Noël, J. 2002. Relations entre la végétation, le milieu physique, les perturbations naturelles et le climat dans le Québec méridional, documents cartographiques : Tome 1. Le système hiérarchique de classification écologique du MRNQ, le milieu physique, les perturbations naturelles et le climat. Direction de la recherche forestière, Ministère des Ressources naturelles, Québec, Que.

- Parent, B. 2003. Ressources et industries forestières : portrait statistique édition 2003. Direction du développement de l'industrie des produits forestiers, Ministère des Ressources naturelles, de la Faune et des Parcs, Québec, Que.
- Paul, K.I., Polglase, P.J., Nyakuengama, J.G., and Khana, P.K. 2002. Change in soil carbon following afforestation. For. Ecol. Manage. 168: 241–257.
- Polglase, P.J., Paul, K.I., Khana, P.K., Nyakuengama, J.G., O'Connell, A.M., Grove, T.S., and Battaglia, M. 2000. Change in soil carbon following afforestation or reforestation. National Carbon Accounting System, Australian Greenhouse Office Tech. Rep. 20.
- Régnière, J., Cooke, B., and Bergeron, Y. 1995. BioSIM: user's manual. Laurentian Forestry Centre, Canadian Forest Service, Sainte-Foy, Que. Inf. Rep. LAU-X-116.
- Richter, D.D., Markewitz, D., Trumbore, S.E., and Welles, C.G. 1999. Rapid accumulation and turnover of soil carbon in a reestablishing forest. Nature (London), 400: 56–58.
- Robitaille, A., and Saucier, J.-P. 1996. Land district, ecophysiographic units and areas: the landscape mapping of the Ministère des Ressources naturelles du Québec. Environ. Monit. Assess. 39: 127–148.
- Rowe, J.S. 1972. Forest regions of Canada. Can. For. Serv. Publ. 1300.
- Saucier, J.-P., Bergeron, J.-F., Grondin, P., and Robitaille, A. 1998. Les régions écologiques du Québec méridional. 3^e version. Un des éléments du système hiérarchique de classification du territoire mis au point par le ministère des Ressources naturelles du Québec. Supplément de l'Aubelle nº 124, Québec, Que.
- SAS Institute Inc. 2003. SAS/STAT user's guide. Version 9.1. SAS Institute Inc., Cary, N.C.

Schiffman, P.M., and Johnson, W.C. 1989. Phytomass and detrital

carbon storage during forest regrowth in the southeastern United States Piedmont. Can. J. For. Res. **19**: 69–78.

- Soil Classification Working Group. 1998. The Canadian system of soil classification. NRC Research Press, Ottawa, Ont.
- Soil Survey Staff. 1988. Soil survey manual. USDA Agric. Handb. 18.
- Thiffault, N., Roy, V., Prégent, G., Cyr, G., Jobidon, R., and Ménétrier, J. 2003. La sylviculture des plantations résineuses au Québec. Nat. Can. (Que.), 127: 63–80.
- Thorn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., and Hendricks, D.M. 1997. Mineral control of soil organic carbon storage and turnover. Nature (London), 389: 170–173.
- Tremblay, S., Ouimet, R., and Houle, D. 2002. Prediction of organic carbon content in upland forest soils of Quebec, Canada. Can. J. For. Res. 32: 903–914.
- Ung, C.-H., Bernier, P.Y., Raulier, F., Fournier, R.A., Lambert, M.-C., and Régnière, J. 2001. Biophysical site indices for shade tolerant and intolerant boreal species. For. Sci. 47: 83–95.
- Végiard, S., and Ung, C.-H. 1993. Statistical inference problems related to the logarithmic transformation in regression: another method for interval estimation. Can. J. For. Res. 23: 871–872.
- Vesterdal, L., Ritter, E., and Gundersen, P. 2002. Change in soil organic carbon following afforestation of former arable land. For. Ecol. Manage. 169: 137–147.
- White, T.M., and Kurz, W.A. 2005. Afforestation on private land in Canada from 1990 to 2002 estimated from historical records. For. Chron. 81: 491–497.
- Wilde, S.A. 1964. Changes in soil productivity induced by pine plantations. Soil Sci. **97**: 276–278.
- Zak, D.R., Grigal, D.F., Gleeson, S., and Tilman, D. 1990. Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. Biogeochemistry, **11**: 111–129.

Appendix A

Table A1. Allometric equations used to estimate aboveground biomass for each species found in the 57 plantations.

	Equation parameter value					
	Equation	$\overline{b_0}$	b_1	<i>a</i> ₁₅	<i>b</i> ₁₅	Reference
Abies balsamea	A5, A6	72.715	2.25	0.0684	1.1302	Roussopoulos and Loomis 1979; Ker 1984
Abies balsamea	A1	0.1746	2.1555			Ker 1984
Acer pensylvanicum	A4	-3.518	2.878			Telfer 1969
Acer rubrum	A1	0.197	2.1933			Ker 1984
Acer rubrum	A4	-4.194	2.094			Telfer 1969
Acer saccharum	A1	0.1599	2.3376			Ker 1980
Acer saccharum ^a	A4	-4.194	2.094			Telfer 1969
Acer spicatum	A5, A6	73.182	2.259	0.1645	1.0485	Roussopoulos and Loomis 1979
Acer spicatum	A1	0.204	2.2524			Whittaker et al. 1979
Alnus rugosa	A5, A6	63.28	2.38	0.1409	1.0225	Roussopoulos and Loomis 1979
Alnus rugosa	A1	0.2612	2.2087			Young et al. 1980
Amelanchier sp. ^b	A5, A6	71.534	2.391	0.0142	1.1037	Roussopoulos and Loomis 1979
Amelanchier sp.	A1	0.2612	2.2087			Young et al. 1980
Betula alleghaniensis	A2	-1.8337	2.1283			Ker 1980
Betula papyrifera	A5, A6	73.316	2.279	0.713	1.0452	Roussopoulos and Loomis 1979; Ker 1984
Betula papyrifera	A1	0.1545	2.3064			Ker 1984
Cornus stolonifera	A5, A6	74.114	2.457	0.0243	1.0828	Roussopoulos and Loomis 1979
Cornus stolonifera ^c	A1	0.0616	2.5094			Perala and Alban 1994
Corylus cornuta	A5, A6	62.819	2.42	0.1894	0.9226	Roussopoulos and Loomis 1979
Crataegus sp.	A5, A6	63.28	2.38	0.1409	1.0225	Roussopoulos and Loomis 1979

Table A1 (concluded).

		Equation parameter value				
	Equation	$\overline{b_0}$	b_1	<i>a</i> ₁₅	<i>b</i> ₁₅	Reference
Crataegus sp.	A1	0.2612	2.2087			Young et al. 1980
Diervilla lonicera	A5, A6	14.211	1.217	0.1062	0.8818	Roussopoulos and Loomis 1979
Fagus grandifolia	A1	0.1958	2.2538			Ker 1980
Fagus grandifolia	A4	-3.647	2.906			Telfer 1969
Juniperus communis	A3	59.205	2.202			Smith and Brand 1983
Larix laricina	A1	0.0946	2.3572			Ker 1980
Lonicera canadensis	A4	-2.427	2.77			Telfer 1969
Nemopanthus mucronatus	A4	-3.04	2.819			Telfer 1969
Picea abies	A1	0.0777	2.472			Harding and Grigal 1985
Picea glauca	A1	0.0777	2.472			Harding and Grigal 1985
Picea glauca	A5, A6	65.757	2.287	0.0715	1.1241	Roussopoulos and Loomis 1979
Picea abies	A5, A6	65.757	2.287	0.0715	1.1241	Roussopoulos and Loomis 1979
Picea mariana	A1	0.1683	2.1777			Ker 1980
Picea mariana	A3	0.5072	1.9246			Wagner and Ter-Mikaelian 1999
Picea rubens	A1	0.166	2.2417			Freedman et al. 1982
Picea rubens ^d	A3	0.5072	1.9246			Wagner and Ter-Mikaelian 1999
Pinus banksiana	A1	0.152	2.273			Ker 1980
Pinus banksiana	A3	0.1694	2.3002			Wagner and Ter-Mikaelian 1999
Pinus resinosa	A1	0.0847	2.3503			Ker 1980
Pinus resinosa	A3	0.1219	2.4618			Wagner and Ter-Mikaelian 1999
Pinus strobus	A1	0.1617	2.142			Ker 1980
Pinus strobus	A3	0.1404	2.2918			Wagner and Ter-Mikaelian 1999
Populus balsamifera ^e	A5, A6	46.574	2.527	0.1294	1.0517	Roussopoulos and Loomis 1979
Populus tremuloides	A1	0.1049	2.391			Ker 1984
Populus tremuloides	A4	-2.92	2.715			Telfer 1969
Prunus pensylvanica	A5, A6	68.041	2.237	0.1151	1.0676	Roussopoulos and Loomis 1979
Prunus pensylvanica	A1	0.1556	2.1948			Young et al. 1980
Prunus sp.	A5, A6	68.041	2.237	0.1151	1.0676	Roussopoulos and Loomis 1979
Prunus virginiana	A1	0.2643	1.7102			Young et al. 1980
Prunus virginiana	A3	9.934	2.92			Brown 1976
Quercus rubra	A1	0.1335	2.422			Perala and Alban 1994
Quercus rubra	A4	-2.299	2.649			Telfer 1969
Ribes sp.	A3	49.001	3.112			Brown 1976
Rubus idaeus	A3	43.992	2.86			Brown 1976
Salix sp.	A1	0.0616	2.5094			Perala and Alban 1994
Salix sp.	A4	-1.519	2.325			Telfer 1969
Sorbus americana	A5, A6	44.394	3.253	0.0263	1.1373	Roussopoulos and Loomis 1979
Sorbus americana ^f	A1	0.1556	2.1948			Young et al. 1980
Thuja occidentalis	A5, A6	68.423	1.863	0.1853	1.0906	Roussopoulos and Loomis 1979; Ker 1984
Thuja occidentalis	A1	0.1148	2.1439			Ker 1980
Vaccinium angustifolium	A4	-3.978	3.706			Telfer 1969
Viburnum alnifolium	A4	-4.079	3.243			Telfer 1969
Viburnum cassinoides	A4	-2.613	2.774			Telfer 1969

Note: Six different equations were used to predict aboveground woody vegetation biomass (B) (DBH is diameter at breast height; DSH is diameter at stump height; D15 is diameter at 15 cm height).

[A1] $B = b_0 \times \text{DBH}^{b1}$ [A2] $B = b_0 + b_1 \times \log \text{DBH}$ [A3] $B = b_0 \times \text{DSH}^{b1}$

[A3] $B = b_0 \times DSH^{-1}$ [A4] $B = b_0 + b_1 \times \log DSH$ [A5] $B = b_0 \times D15^{b1}$ [A6] D15 = (DSH - a_{15})/ b_{15} "The equation for A. rugosa was used. "The equation for A. rugosa was used.

^cThe equation for *Salix* sp. was used. ^dThe equation for *P. mariana* was used.

^eThe equation for *Populus* sp. was used.

^fThe equation for *P. pensylvanica* was used.

References

- Brown, J.K. 1976. Estimating shrubs biomass from basal stem diameters. Can. J. For. Res. 6: 153–158.
- Freedman, B., Duinker, P.N., Barclay, H., Morash, R., and Prager, U. 1982. Forest biomass and nutrient studies in central Nova Scotia. Can. For. Serv. Marit. For. Res. Cent. Inf. Rep. M-X-134.
- Harding, R.B., and Grigal, D.F. 1985. Individual tree biomass estimation equations for plantation-grown white spruce in northern Minnesota. Can. J. For. Res. 15: 739–739.
- Ker, M.F. 1980. Tree biomass equations for ten major species in Cumberland County, Nova Scotia. Can. For. Serv. Marit. For. Res. Cent. Inf. Rep. M-X-108.
- Ker, M.F. 1984. Biomass equations for seven major Maritimes tree species. Can. For. Serv. Marit. For. Res. Cent. Inf. Rep. M-X-148.
- Perala, D.A., and Alban, D.H. 1994. Allometric biomass estimators for aspen-dominated ecosystems in the Upper Great lakes. USDA For. Serv. Res. Pap. NC-134.

- Roussopoulos, P.J., and Loomis, R.M. 1979. Weights and dimensional properties of shrubs and small trees of the Great Lakes conifer forest. USDA For. Serv. Res. Paper NC-178.
- Smith, B.W., and Brand, G.J. 1983. Allometric biomass equations for 98 species of herbes, shrubs, and small trees. USDA For. Serv. Res. Pap. NC-299.
- Telfer, E.S. 1969. Weight-diameter relationships for 22 woody plant species. Can. J. Bot. 47: 1851–1855.
- Wagner, R.G., and Ter-Mikaelian, M.T. 1999. Comparison of biomass component equations for four species of northern coniferous tree seedlings. Ann. Sci. For. (Paris), 56: 193–199.
- Whittaker, R.H., Likens, G.E., Bormann, F.H., Eaton, J.S., and Siccama, T.G. 1979. The Hubbard Brook ecosystem study: forest nutrient cycling and element behavior. Ecology, **60**: 203–220.
- Young, H.E., Ribe, J.H., and Wainwright, K. 1980. Weight tables for tree and shrub species in Maine. Life Sci. Agric. Exp. Stn. Misc. Rep. 230.