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Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada

Wenjun Chen, Jing M. Chen, David T. Price, and Josef Cihlar

Abstract: Quantification of the effects of stand age on its net primary productivity (NPP) is critical for estimating forest NPP and carbon budget at regional to global scales. This paper reports a practical method for quantifying age–NPP relationships using existing normal yield tables, biomass equations, and measurements of fine-root turnover and litterfall. Applying this method, we developed mean age–NPP relationships for black spruce (*Picea mariana* (Mill.) BSP) stands in Ontario. We define "mean age–NPP relationship", as the changes in NPP that occur with age under long-term mean environmental conditions. These relationships indicate that NPP at more productive sites culminates to a higher value and at an earlier age and also declines more rapidly thereafter. A further component analysis indicates that the decrease in biomass growth of woody tissues is the main contributor to the decline with age. Finally, error assessment suggests that the uncertainty in NPP estimates can be substantially reduced with a better quantification of fine-root turnover and litterfall, which are the two dominant NPP components, particularly in the later stages of stand development. With new techniques now available, more accurate measurement of these components is possible, and thus strongly recommended.

Résumé : La quantification des effets de l'âge du peuplement sur sa productivité primaire nette (PPN) est critique dans l'estimation de la PPN de la forêt et du bilan du carbone aux échelles régionale et globale. Cet article rend compte d'une méthode pratique pour quantifier les relations entre la PPN et l'âge à partir des tables de rendement normal existantes, d'équations de biomasse et de mesures du renouvellement des racines fines et de la litière. En appliquant cette méthode, nous avons développé des relations moyennes entre la PPN et l'âge pour les peuplements d'épinette noire (*Pice mariana* (Mill.) BSP) en Ontario. La « relation moyenne entre la PPN et l'âge » représente les changements de PPN avec l'âge dans des conditions environnementales moyennes à long terme. Ces relations montrent que la PPN culmine à une valeur plus élevée et à un âge plus précoce et décline aussi plus rapidement par la suite dans les sites les plus productifs. Une analyse plus poussée par composantes montre que la diminution en croissance de la biomasse des tissus ligneux représente la principale composante qui explique le déclin avec l'âge. Finalement, une estimation de l'erreur indique que l'incertitude reliée aux évaluations de la PPN peut être substantiellement réduite avec une meilleure quantification du renouvellement des racines fines et de la litière, lesquels constituent les deux composantes dominantes de la PPN, en particulier dans les stades les plus tardifs du développement du peuplement. La disponibilité de nouvelles techniques permet de mesurer ces composantes avec plus précision; ce qui est donc fortement recommandé.

[Traduit par la Rédaction]

1. Introduction

The global terrestrial carbon (C) cycle has played, and will continue to play, an important role in determining atmospheric CO_2 concentration and, therefore, influences the global climate system (Houghton et al. 1996). At regional to global scales, the terrestrial C budget is net of C gain through primary productivity (NPP) and C loss due to soil

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heterotrophic respiration and loss from disturbances, such as forest fires. Forest fires not only result in C loss in the year of occurrence but also have substantial post-disturbance impacts on NPP and, consequently, on C budget through resetting the age of burned stands to zero. Other disturbances, such as harvesting and insects-induced mortality, have similar effect on stand age. Work over the last 10 years has demonstrated that such post-disturbance impacts on C budget at both local and national scales can be substantial (e.g., Kurz et al. 1992; Kurz and Apps 1999; Price et al. 1997). Yet, most process-based NPP and C budget models have so far considered only the effects of environmental factors, such as climate, soil conditions, atmospheric CO_2, and nitrogen deposition (e.g., McGuire et al. 1992; Rastetter et al. 1997; Liu et al. 1999). The primary reason why effects of disturbances are not incorporated in process-based NPP and C budget models is the lack of quantitative knowledge about age effects on NPP, and lack of spatial data on age and species distribution.

How can the effects of forest stand age on NPP be quantified? Age-related changes in the productivity of forest stands

have been known for centuries. In recent decades, various physiological explanations have been proposed (Gower et al. 1996; Murty 1996; Hunt et al. 2000). Ryan et al. (1997) reviewed these hypotheses in detail, which include (*i*) changes in photosynthesis with stand development (reduced leaf area and photosynthetic capacity); (*ii*) changes in nutrient supply; (*iii*) change in respiration; (*iv*) changes in C allocation; and (*v*) change in hydrological function. Recently, Smith and Long (2001) suggested structural changes, especially canopy closure and associated changes in foliage arrangement within the canopy, are responsible for age-related decline in forest production. The experimental results indicate that all these factors contribute to changes in NPP with age, although their relative importance varies from one ecosystem to another. Clearly, many more studies are needed before mechanistic simulation of the effects of stand age on NPP is possible for all major species.

On the other hand, foresters and forestry researchers have developed and published stand yield tables of wood volume for forest management purposes since the late 18th century (Würth et al. 1997). Stand yield tables contain valuable information about effects of age on NPP. By combining them with biomass allometric equations and other field measurements, we can derive age–NPP relationships. Such age–NPP relationships are "averaged" for long-term mean environmental conditions, because averaging and smoothing procedures are generally applied in yield tables development. Therefore, to estimate actual NPP of a stand in a specific year, effects of changes in environmental factors must be superimposed on the effect of age given by the mean age–NPP relationships (e.g., J.M. Chen et al. 2000; W.J. Chen et al. 2000*a*, 2000*b*).

Until now, systematic age–NPP relationships for major forest species were not available for Canada. The main objective of this paper is to develop a practical methodology for quantifying mean age–NPP relationships of black spruce stands (*Picea mariana* (Mill.) BSP) in Ontario, Canada. We will apply this method to develop mean age–NPP relationships for other major Canadian forest species, to be reported elsewhere. These age–NPP relationships not only allow a better quantification of NPP, and consequently of C budget, and also could serve as an empirical reference for process-based studies of age effects on NPP. Details of the methodology are given in section 2, followed by data sources. In section 4, we report the age–NPP relationships determined for black spruce stratified by site index. Uncertainties with this approach for estimating effects of age on NPP are also discussed.

2. Methodology

We estimate the NPP of a forest over a year as the sum of four components (Perry 1994). The first is the growth in tree tissues (ΔB_{tree}), including stems (ΔB_s = stemwood (ΔB_{sw}) + stem bark (ΔB_{sb})), branches (ΔB_b), foliage (ΔB_f), and roots (ΔB_r). The second component is tissues that are shed from the tree as litter (L_{tree}), including foliage and twig litterfall (L_f) and fine-root turnover (L_{fr}). The third component is tree mortality (M_{tree}), including all components of trees, namely stems (M_s), branches (M_b), foliage (M_f), and roots (M_r). The final component is the contribution of understory vegetation

and (or) moss to NPP. Foliage tissues consumed by heterotrophs, such as insects, are often substantial (Perry 1994), so this should be included in foliage production, if foliage litterfall is measured. On the other hand, if the foliage production is estimated from foliage biomass and its turnover rate measured in a year when defoliation is insignificant, the amount of foliage consumed by heterotrophes is automatically included, so there is no need for explicit consideration of heterotrophe consumption. Hence, NPP is given by

[1] $\mathrm{NPP} = \Delta B_{tree} + L_{tree} + M_{tree} + \mathrm{NPP}_{und}$

where $\Delta B_{tree} = \Delta B_s + \Delta B_b + \Delta B_f + \Delta B_r$, $L_{tree} = L_f + L_{fr}$, $M_{tree} = M_s + M_b + M_f + M_r$, and NPP_{und} is the understory NPP. For the convenience of C budget model application, we convert biomass into C content using the following conversion factors: 0.5 for stem, branch, and coarse roots and 0.45 for foliage and fine roots (Gower et al. 1997).

2.1. Biomass growth

With known values of a biomass component B_x at two ages A_{i-1} and A_i (where i is in integral), the mean annual biomass growth, ΔB_x, can be calculated as

[2] $\Delta B_x \left(\dfrac{A_i + A_{i-1}}{2} \right) = \dfrac{B_x(A_i) - B_x(A_{i-1})}{A_i - A_{i-1}}$

where subscript x can be stems, s; branches, b; foliage, f; or roots, r.

Yield tables usually include age (A), diameter at breast height (D), height (H), stand density (S), and gross total volume of stemwood (V) (e.g., Plonski 1981). With these data, stem biomass at age A_i can be calculated in two different ways. The first is to use the total stem volume given in the yield tables and to calculate stem biomass at age A_i from $B_{sw}(A_i) = V(A_i)\rho_w$, where ρ_w is the green wood density (i.e., dry biomass divided by the "green" volume). The second way is to use the data of D, H, and S in yield tables and biomass equations (e.g., Evert 1985, see below). The data compiled by Gonzalez (1990) for 2153 black spruce sample trees in Canada show a substantial variation in green wood density, ranging from 304 to 625 kg·m^{-3}. Yet, this variation shows no clear relationship with stand age and growth rate, as reported by Singh (1986) for the Prairie Provinces and by Hall (1984) for Newfoundland. Consequently, a constant (mean) wood density can be used for converting gross volume to stemwood biomass. To further test this hypothesis, we compared stemwood biomass calculated using both methods for black spruce stands in Ontario (Fig. 1). For the second method, the effect of changes in tree sizes on stemwood biomass needs was considered, following the approach used by Penner et al. (1997). We constructed a hypothetical stand by assuming D and H are normally distributed variables, with a mean equal to average D and H given in the yield tables, and a variance equal to 20% of the mean values. In Fig. 1, every point represents an entry with a given age and site index (SI, height in metres at 50 years) in the yield tables for black spruce in Ontario (Plonski 1981; Payandeh 1990). These data indicated that for black spruce stands in Ontario of all age ranges and site qualities, a constant wood density of 445 kg·m^{-3} would be acceptable.

Biomass values of branch, foliage, and stem bark cannot be estimated directly using the yield tables. Following Ruark and Bockheim (1988) and Gower et al. (1997), we estimate them from ratios of branch, foliage, and stem bark biomass to stemwood biomass, using D and H in the yield tables and allometric equations. Ideally, we should use allometric equations corresponding to the yield tables used. For example, for yield tables in Ontario, we should use biomass equations developed by Alemdag (1983). Unfortunately, the biomass equations of Alemdag (1983) imposed a constant allometric ratio (CAR), which may cause a significant error in estimating branch and foliage biomass (Ruark and Bockheim 1988). Ruark and Bockheim (1988) suggested that this error may be reduced by using variable allometric ratio (VAR). Many investigators have developed VAR biomass equations for different regions in Canada. Yet, these biomass equations often have different forms, limited sample sizes, and different applicable ranges. Instead of trying to synthesize these reported biomass equations, Evert (1985) developed a set of uniform, nationwide single-tree VAR biomass equations for black spruce using sample tree data collected from all regions of Canada (e.g., Ker 1984; Standish et al. 1985; Manning et al. 1984; Singh 1984; Lavigne 1982), as follows:

Fig. 1. Comparison of stemwood biomass of black spruce stands in Ontario, calculated using biomass equation of Evert (1985) and using forest volume and wood density of 445.2 kg·m^{-3}.

$$[3] \quad b_{sw} = 0.2 + 1.9353 \times 10^{-2}\, D^2H - 2.65 \times 10^{-4}\, D^3H + 2.013 \times 10^{-6}\, D^4H$$

$$[4] \quad b_{sb} = 0.05 + 1.335\,76 \times 10^{-3}\, D^2H + 7.267\,87 \times 10^{-3}\, D^{1.5}H - 6.972\,25 \times 10^{-5}\, D^2H^2 + 4.307\,16 \times 10^{-8}\, D^2H^4$$

$$[5] \quad b_c = 0.8 + 4.401\,73 \times 10^{-2}\left(\frac{D^3}{H}\right) + 9.638\,92 \times 10^{-9}\left(\frac{D^3}{H}\right)^2 - 2.6208 \times 10^{-9}\left(\frac{D^3}{H}\right)^3$$
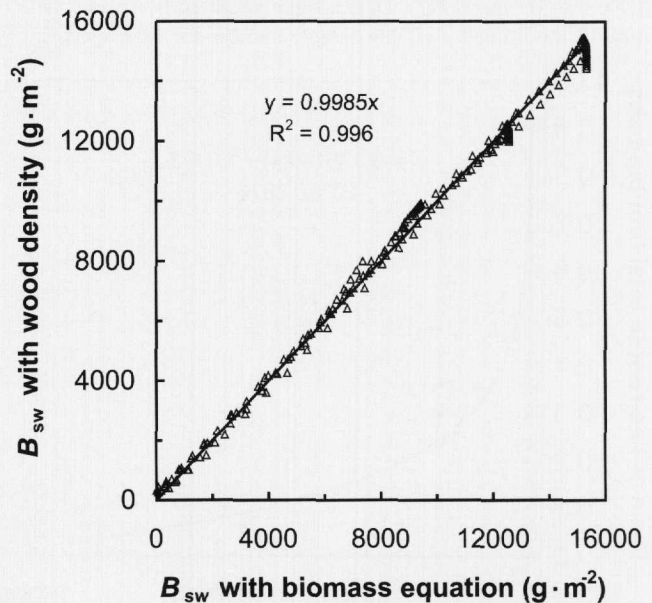
where b_{sw}, b_{sb}, and b_c are biomasses of stemwood, stem bark, and crown ($b_c = b_b$ (branch) + b_f (foliage)), in kilograms per tree; and D and H are in centimetres and metres, respectively. The corresponding standard errors (SEs) of these biomass estimates were 13.8, 30.8, and 59.8%, respectively, from a sample size (N) of 1769 trees (Evert 1985). We further divided the crown biomass into branches and needles, by fitting a regression equation to the ratios of b_f to b_b given by VAR biomass equations of Ker (1984), Standish et al. (1985), Manning et al. (1984), Singh (1984), Lavigne (1982), and Gower et al. (1997), as follows:

$$[6] \quad \frac{b_f}{b_b} = 0.6789 - 0.0775\ln(H)$$

Stand-level biomass values (g biomass or g C·m^{-2} of B_{sb}, B_b, and B_f are then given by $B_{sb} = B_{sw}b_{sb}/b_{sw}$, $B_b = B_{sw}b_b/b_{sw}$, and $B_f = B_{sw}b_f/b_{sw}$, respectively. Again, in calculating these ratios of b_{sb}/b_{sw}, b_b/b_{sw}, and b_f/b_{sw}, the above hypothesized stand was utilized to include the effect of changes in tree sizes on b_{sw}, b_{sb}, b_b, and b_f.

We calculate total root biomass B_r and fine-root biomass B_{rf} (= B_r – coarse root biomass B_{rc}) using relationships between B_r and aboveground biomass B_a (= $B_s + B_b + B_f$), and between B_{rf} and B_r (see eq. 8). Based on data obtained for black spruce stands in Saskatchewan and Manitoba (Steele

et al. 1997), in Alaska (Ruess et al. 1996), and in Newfoundland (Cannell 1982), we established a relationship between B_r and B_a:

$$[7] \quad B_r = 0.454 B_a$$

with an SE of 20.2% and $N = 5$. Fine roots are generally defined as nonwoody, small-diameter roots and mycorrhizae. Upper values for fine-root diameters vary among published studies and generally range from <1 to ≤5 mm, because fine-root morphology and size vary among species and even within species across sites (Nadelhoffer and Raich 1992). When these different definitions are used, the relationship between B_{rf} and B_r can differ substantially. Compiling data from literature (Kurz et al. 1996; Steele et al. 1997; Ruess et al. 1996; Finer et al. 1997; Malik and Timmer 1998), we developed a relationship between B_{rf} and B_r for all forest species with the upper limit of fine-root diameter being ≤5 mm as follows:

$$[8] \quad B_{rf} = [1.3173 - 0.135\ln(B_r)]B_r$$

with an SE of 30.5% and $N = 35$ (Fig. 2).

2.2. Litterfall and fine-root turnover

Coniferous needle life-spans vary within and among species in relation to internal and external factors, including

Fig. 2. Ratio of fine-root biomass to total root biomass as a function of total root biomass, based on data in literature (Kurz et al. 1996; Steele et al. 1997; Ruess et al. 1996; Finer et al. 1996; Malik and Timmer 1997). Data are not stratified by species because of the limited available sample number for each species.

$y = -0.1351 \ln(x) + 1.3173$
$R^2 = 0.8876$
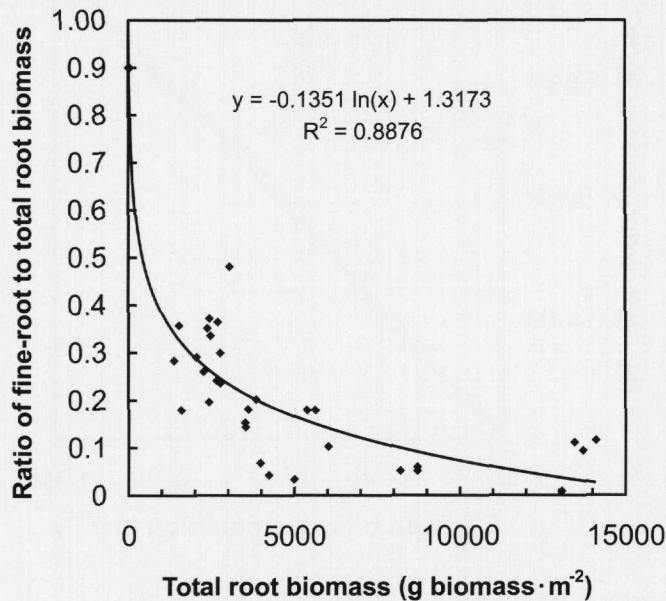
temperature, light, water, nutrients, insects, diseases, and air pollution (Reich et al. 1995). For example, needle life-span is usually shorter on fertile sites and in warm sunny micro-environments, although these patterns can be altered by factors such as drought, diseases, insects, or air pollution (Reich et al. 1995). Unfortunately, measurements of needle life-span, and the corresponding turnover rate, are generally made only in specific locations rather than across gradients of all these factors. For black spruce, measurements show that the foliage turnover rate is 0.069–0.083 year^{-1} in the southern BOREAS study area in Saskatchewan, compared with 0.061–0.075 year^{-1} in the northern BOREAS study area in Manitoba (Gower et al. 1997). It is doubtful whether these two sites represent the full range of conditions affecting needle turnover rate, but lacking any other data for black spruce, we used a constant mean value for needle turnover rate of 0.0722 year^{-1} for black spruce in this study. Similarly, we used a constant mean value of 0.0241 year^{-1} for branch biomass turnover, based on measurements at these same sites (Gower et al. 1997).

These same factors that affect needle life-span may also affect fine-root life-span. For example, Hendrick and Pregizer (1993) reported that the life-span of sugar maple (*Acer saccharum* Marsh.) fine roots was shorter at a southern site than at a northern site in Michigan. However, a comparison by Ruess et al. (1996) of fine-root turnover rates in white spruce (*Picea glauca* (Moench) Voss) growing on a fertile upland site and a less fertile floodplain site indicated higher turnover rates on the less fertile site. The situation is also complicated by different definitions of fine roots (i.e., <1, 2, or 5 mm), and different methods for estimating fine-root production (Nadelhoffer and Raich 1992; Ruess et al. 1996; Steele et al. 1997). Commonly used methods for determining fine-root production include sequential coring,

ingrowth cores, maximum–minimum, and minirhizotron (Nadelhoffer and Raich 1992; Ruess et al. 1996; Steele et al. 1997). The methods of sequential coring, ingrowth core, and maximum–minimum generally underestimate fine-root production because fine-root growth and mortality typically occur simultaneously (Publicover and Vogt 1993; Steele et al. 1997). Data obtained by Steele et al. (1997) using minirhizotrons clearly showed that fine-root growth and mortality occurred concurrently for black spruce, particularly during summer. Therefore, data from minirhizotrons evidently provide more accurate estimates of fine-root production. Using these minirhizotron data and <5 mm as a definition of fine roots, we calculate fine-root turnover rate at the northern BOREAS site to be approximately 0.21 year^{-1}, compared with 0.40 year^{-1} at the southern BOREAS site. Because of all the uncertainties in these estimates, however, we adopted a constant rate for fine-root turnover of 0.30 year^{-1} in this study.

2.3. Mortality

Mortality occurs for numerous reasons, but in an otherwise vigorous and healthy stand, the main cause is competition from neighbouring trees. Therefore, the mean mortality rate of a stand between ages A_{i-1} to A_i can be estimated from decreases in stand density:

$$[9] \qquad M_{\text{tree}}\left(\frac{A_i + A_{i-1}}{2}\right) = \alpha \, \frac{B_{\text{tree}}(A_{i-1})}{S(A_{i-1})} \, \frac{[S(A_{i-1}) - S(A_i)]}{A_i - A_{i-1}}$$
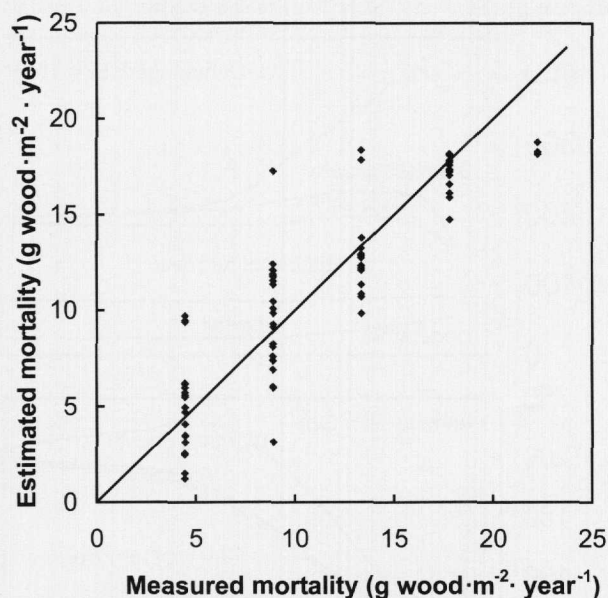
where α is a coefficient. The value of α should be less than 1, because trees dying due to competition are generally smaller than the dominant trees that survive. Plonski's (1981) yield tables for black spruce include stem volume loss due to death of suppressed trees. Figure 3 shows that the estimated mortality for stemwood, using eq. 9 with α set to 0.296, agrees well with the measured mortality given in yield tables (SE = 23.5%, $N = 76$) and, thus, was applied to all stands reported in this paper. Values of M_s, M_b, M_f, and M_r were calculated by replacing B_{tree} in eq. 9 with B_s, B_b, B_f, and B_r, respectively.

2.4. NPP of understory vegetation

Understory vegetation is not included in forest yield tables and biomass equations. Gower et al. (1997) reported that in 1994, NPP of understory vegetation (i.e., shrubs and herbs) and of bryophytes (i.e., mosses and lichens) were 13 and 12 g C·m^{-2}·year^{-1} at a site in Saskatchewan and 0 and 12 g C·m^{-2}·year^{-1} at a site in Manitoba, respectively. For the Manitoba site, Frolking (1997) estimated a similar moss NPP of 13 g C·m^{-2}·year^{-1} in 1994. Over a longer period (1968–1989), Frolking (1997) estimated a mean moss NPP of 35 g C·m^{-2}·year^{-1} for the Manitoba site, consistent with Canada-wide mean values of 16–60 g C·m^{-2}·year^{-1} reported by Weetman and Timmer (1967).

Rapalee et al. (1998) estimated C accumulation rates in the soil surface layer of black spruce stands with different drainage classes and stand ages in Manitoba. The C accumulation rates were similar for drainage classes ranging from poorly to moderately well drained but decreased with stand age (Fig. 4). It should be noted that C accumulation in the soil surface layer is not equivalent to understory NPP, be-

Fig. 3. Comparison of estimated and measured mortality for stemwood. The slope coefficient $\alpha = 0.297$, $r^2 = 0.77$ with sample number being 76.

Fig. 4. Variations of C accumulation rates in the surface layer with age, at black spruce sites with different drainage classes in Manitoba. Data are from Rapalee et al. (1998).

cause it includes some litterfall from the tree canopy and also does not account for decomposition of dead plant material produced by the understory and moss layers. Hence, C accumulation in the surface layer can be considered at best only a rough approximation of real understory and bryophyte NPP. Nevertheless, because no other reliable data are available and because these C accumulation rates agree well with previously reported understory NPP values for Canada (Frolking 1997; Weetman and Timmer 1967), we used an equation fitted to these C accumulation data to represent the relationship between age, A, and aboveground understory NPP, NPP_{und}, in g $C \cdot m^{-2} \cdot year^{-1}$, as follows:
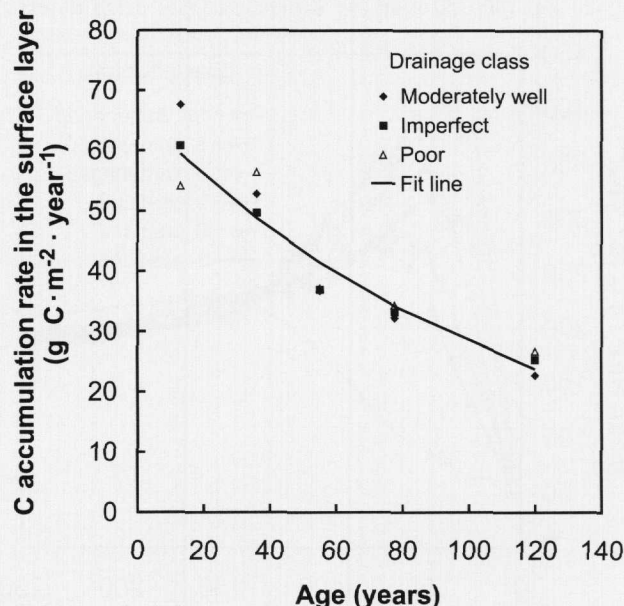
$$[10] \quad NPP_{und} = e^{-0.00858A}$$

The equation was applied for all ages in the range $13 < A < 120$. Outside this range, constant values of 59 g $C \cdot m^{-2} \cdot year^{-1}$ for $A < 13$ and 24 g $C \cdot m^{-2} \cdot year^{-1}$ for $A > 120$ were assigned.

3. Data sources

Since the main goal of this study was to develop mean age–NPP relationships for black spruce stands in Ontario, we used the normal yield tables developed by Plonski (1981) and Payandeh (1990). Plonski's yield tables were developed for unmanaged black spruce stands. These yield tables provide H, D, S, and V at different ages for three site index classes: class 1 with $SI = 11$, class 2 with $SI = 8$, and class 3 at $SI = 5$. Actual stand mean heights at 50 years are 11.0, 8.2, and 5.1 m for SI classes 1, 2, and 3, respectively. Values of V for suppressed trees are also available. For SI classes 1 and 2, the age range of the volume data was 20–150, compared with 30–150 for SI class 3. The age interval in these yield tables is 5 years.

Payandeh's yield tables were developed for peatland black spruce stands in northern Ontario. In these yield tables, data are available for all stand variables, except volume of sup-

pressed trees, for ages from 20 to 150 years, with an age interval of 10 years. Tables for three site indices, 9, 6, and 3 are provided with actual stand mean heights at 50 years of 8.6, 6.1, and 3.4 m, respectively.
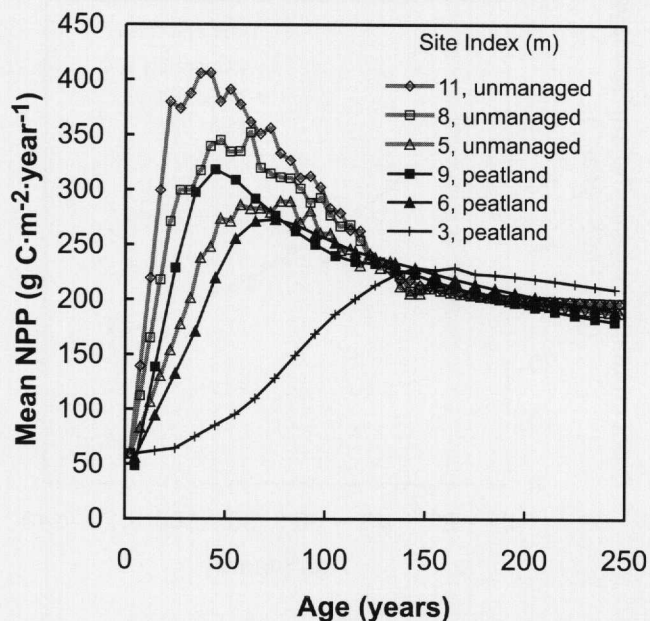
4. Results and discussion

4.1. Effects of stand age on NPP

Figure 5 shows the mean age–NPP relationships derived for unmanaged and peatland black spruce stands with different SI values in Ontario. The original yield tables allowed NPP to be estimated for stands in the range 20–150 years. Estimation of the effects of stand age on NPP for $A > 150$ years and $A < 20$ years is important for C budget studies (e.g., Kurz et al. 1999; J.M. Chen et al. 2000; W.J. Chen et al. 2000a, 2000b). Therefore, we extrapolated the NPP relationships for $A > 150$ and $A < 20$. For $A > 150$ years, the extrapolation was carried out based on fitted relationships between A and ΔH (= $H(A_i) - H(A_{i-1})$), ΔD (= $D(A_i) - D(A_{i-1})$), or ΔS (= $S(A_i) - S(A_{i-1})$) for the age range of 100–150. For $100 < A < 150$, ΔH, ΔD, and ΔS decrease consistently with A towards zero for all SI values. These monotonic decreases in ΔH, ΔD, and ΔS with age indicate the values of H, D, and S can be reasonably extrapolated before the stand eventually breaks up. The values of stemwood biomass for $A > 150$ were determined using the stemwood biomass equation. For $A < 20$ years, a simple linear extrapolation of overstory NPP was performed, with overstory NPP at $A = 0$ set to zero.

For a given SI, mean NPP generally increases with age initially, reaches a maximum, and then declines to a relatively stable value. For the most productive site class studied in this paper ($SI = 11$), estimated NPP reaches a maximum at around 40 years and then gradually decreases to about 50% of maximum at 150 years. The magnitude of this decrease is smaller for less productive stands, and for the least productive peatland stands ($SI = 3$), NPP increases continu-

Fig. 5. Mean age–NPP relationships of unmanaged and peatland black spruce stands with different SI in Ontario, under long-term mean environmental conditions. NPP values over the age ranges of 0–20 and 150–250 years are extrapolated (see detail in text).

Fig. 6. NPP components according to biomass as biomass growth, mortality, fine-root turnover, litterfall, and aboveground understory, for the most productive site (SI = 11 m) and least productive peatland site (SI = 3 m) in this study.

ously up to 150 years. For ages greater than 150 years, the extrapolated data suggest that NPP declines gradually for all SI but will not approach zero within a typical black spruce life-span. The primary reason for this is that for growth past 150 years, NPP is allocated almost exclusively to foliage and fine-root production with short turnover periods, as discussed in the next section. These two fast-cycling NPP components are essential to keep the stands alive. We emphasize, however, that effects of stand break-up or species succession on NPP and C dynamics are not considered here. In reality, these effects may alter the pattern of age–NPP relationships substantially, particularly at older ages. On the other hand, in the absence of fire, black spruce stands can persist for periods considerably longer than 150 years, either because the trees are long lived or because spruce seedlings can regenerate successfully in the shade of older trees. Nevertheless, studies to quantify the effects of stand break-up and succession are essential to improve our understanding of age–NPP dynamics in older stands, particularly of early successional species such as pine and aspen.

As expected, NPP differs substantially both in terms of magnitude and the timing of particular phases, for sites with different SI values. On the sites with highest SI, maximum NPP is greatest and occurs earliest. These large NPP variations caused by site quality indicate the need for caution in interpreting age effects on NPP from measured NPP values in an age chronosequence. If measurements of NPP are made at sites of different SI values, they should be stratified according to SI values before being used for constructing age–NPP relationships. In addition, the effects of interannual variations in environmental factors should also be removed, because they can easily be larger than the effects of age over an age interval such as 5 or 10 years (Peng and Apps 1999). In comparison, yield tables are generally stratified according to SI values, and the effects of interannual environmental
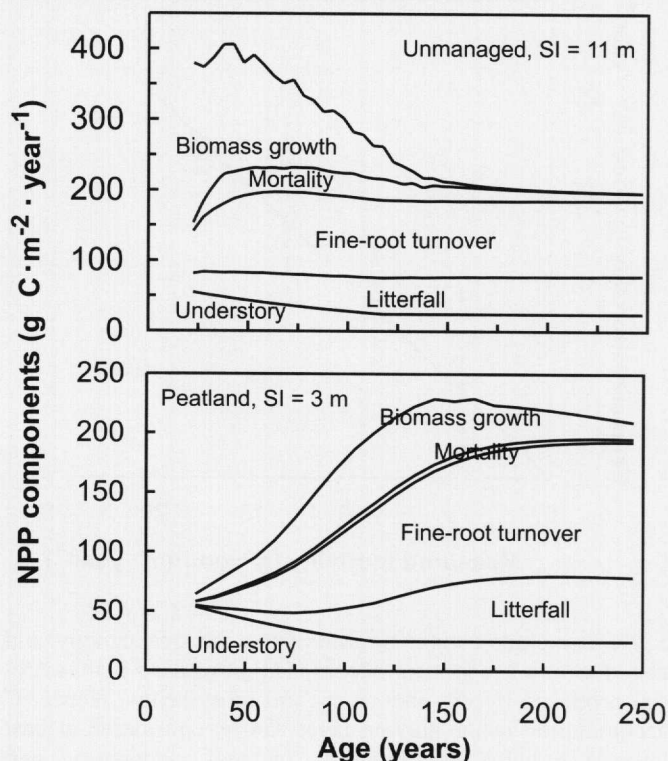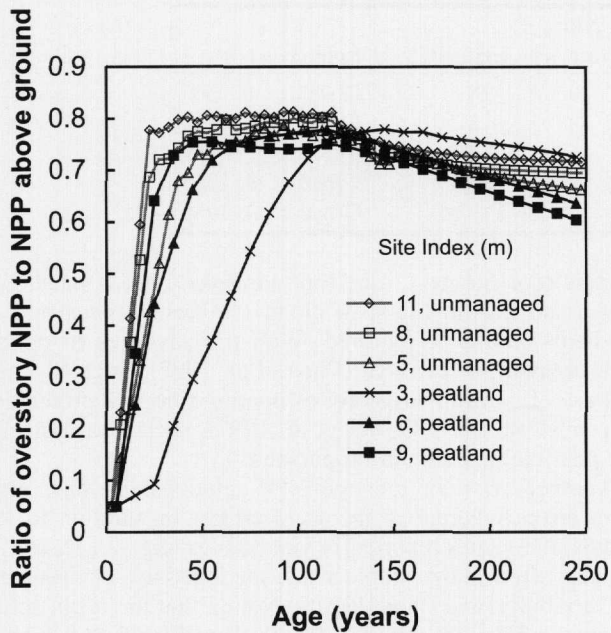
variability on yield table indicators (such as *D*, *H*, *S*, and *V*) are greatly reduced through averaging and (or) smoothing procedures. Hence, we expect that the age–NPP relationships developed here should be good indicators of the long-term average trends in NPP. To apply these age–NPP relationships to extended areas such as a forest management unit, spatially explicit maps of species and site index would also be needed (Ung et al. 2001).

4.2. Effects of stand age on NPP components

The decline in NPP with age is caused mainly by decreases in biomass growth in woody components (i.e., stems, branches, and coarse roots) (Fig. 6). Biomass growth of stems, large branches and coarse roots is the largest component of NPP for stands with SI = 11 m when they are young (age <60 years). Afterwards, fine-root turnover and litterfall become the dominant components. The mortality rate (stems/ha per year) increases initially with age, reaches a maximum, and then decreases. This occurs because, in the initial stages of stand development, many trees are dying, but they are generally very small. In the young stand, biomass growth, litterfall, fine-root turnover, and mortality all increase with age. This is most evident on the least productive sites with SI = 3 m (Fig. 6).

In the early stages of stand development (i.e., before the stand reaches "canopy closure"), understory vegetation is the dominant contributor to aboveground NPP (Fig. 7). In Fig. 7, we compare only the aboveground components, because measurements of fine-root production include both overstory and understory vegetation. The understory NPP then de-

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Fig. 7. Ratio of aboveground overstory NPP to total aboveground NPP as a function of age and SI for black spruce stands in Ontario, Canada.


Fig. 8. Carbon allocation coefficients for stem plus branch, foliage, coarse roots, and fine roots of black spruce stands at the most productive site (SI = 11 m) and the least productive peatland site (SI = 3 m) in Ontario, Canada.

creases with age, although it plays a proportionately larger role in low-productivity stands, presumably because the trees reach canopy closure more slowly and, thus, allow suitably adapted understory species more opportunity to capitalize on the available resources, until the tree cover shades them out. Overstory black spruce trees establish within 20–30 years for all SI (except the peatland stand with SI = 3 m) and, thereafter, become the dominant contributor to total aboveground NPP. For stands aged 30–100 years other than SI = 3 m, overstory black spruce trees contribute 70–80% of total aboveground NPP, although this percentage decreases gradually in the late development stage, as overstory NPP decreases.

4.3. Effects of stand age on C allocation coefficients

Carbon allocation coefficients are the fractions of NPP partitioned among the various biomass components (stems, branches, foliage, coarse roots, and fine roots). Figure 8 shows the C allocation coefficients of overstory NPP in the most and least productive black spruce stands (SI of 11 and 3 m, respectively). As expected, allocation to woody components (i.e., stems, branches, and coarse roots) is higher for the more productive site, and conversely, a greater proportion of available NPP is allocated to fine roots and foliage in the less productive stand. This is probably because, on sites with high water table and low nutrient availability (typical of peatlands), exploitation of available nutrients becomes a key limitation to growth. Thus, the trees must invest much of NPP in root production, and relatively little is available for foliage and wood production. The more productive sites also feature a more rapid decrease with age in C allocation coefficients to woody tissues, whereas for the least productive site, allocation to woody components appears to increase slightly during the first 50–100 years. For all SI, however, allocation to woody components declines in the later stages of development. Conversely, C allocation to foliage and fine
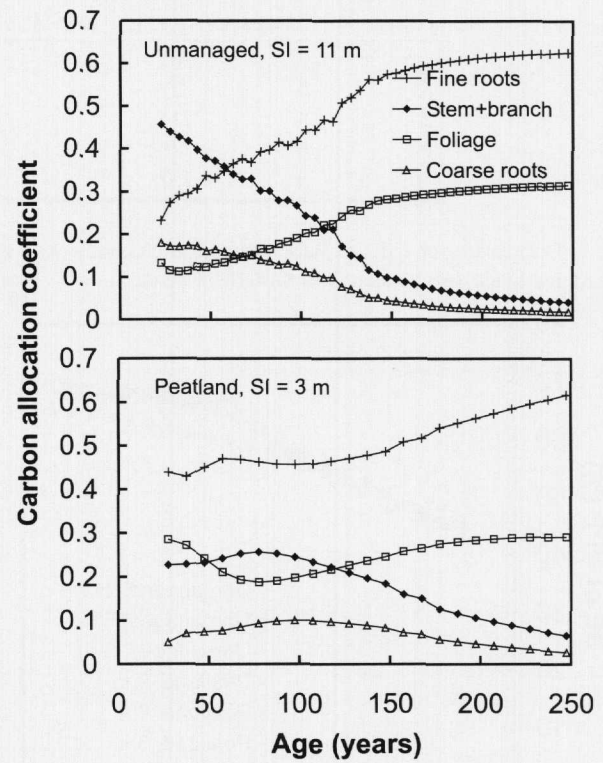
roots appears to increase steadily with age and does not stabilize within 250 years. These results indicate that C allocation coefficients can vary considerably both with age and site quality. Friedlingstein et al. (1999) developed a C budget model in which allocation coefficients were allowed to vary, but in general, C budget models assume constant C allocation coefficients (e.g., McGuire et al. 1992; Murty et al. 1996; W.J. Chen et al. 2000a). Our results may serve as a basis for improving C allocation in C budget simulation studies.

When averaged for all SI and all ages, the C allocation coefficients are approximately 18, 22, 8, and 52%, for stems and branches, leaves, coarse roots, and fine roots, respectively. When the understory vegetation is included, allocation to above- and below-ground components is 48 and 52%, respectively.

4.4. Assessment of estimation error

As discussed in section 2.1, SEs were 13.8, 30.8, 59.8, and 59.8% for estimates of biomass in stemwood, stem bark, foliage, and branches, respectively. The SE for the estimate of total root biomass derived from aboveground biomass was 34%, while the SE for estimating fine-root biomass from total root biomass was 30.5%. The relationship between total root biomass and fine-root biomass is not linear; a 34% error in total root biomass estimation results in an error of 12.7% in fine-root biomass. Therefore, the overall SE for fine-root biomass estimation is about 43%. If these estimation errors are independent of age and SI, then SE for growth of each biomass component should be the same as those determined

Table 1. Comparison of mean NPP calculated using yield-table based method of this study with NPP measured by Gower et al. (1997) in Saskatchewan and Manitoba, by Ruess et al. (1996) in Alaska, and by Grigal et al. (1985).

Stand age (years)	SI (m)	Mean NPP (g C·m^{-2}·year^{-1})	Measured NPP (g C·m^{-2}·year^{-1})	Error (%)	Reference
115	3	201	266	−24.6	Gower et al. 1997
155	3	227	219	3.7	Gower et al. 1997
225	3	214	225	−4.7	Ruess et al. 1996
75	6	273	315	−13.4	Grigal et al. 1985
110	9	237	263	−9.8	Grigal et al. 1985

Fig. 9. Standard error (SE) of NPP estimation changing with age and SI for black spruce stands in Ontario, Canada.
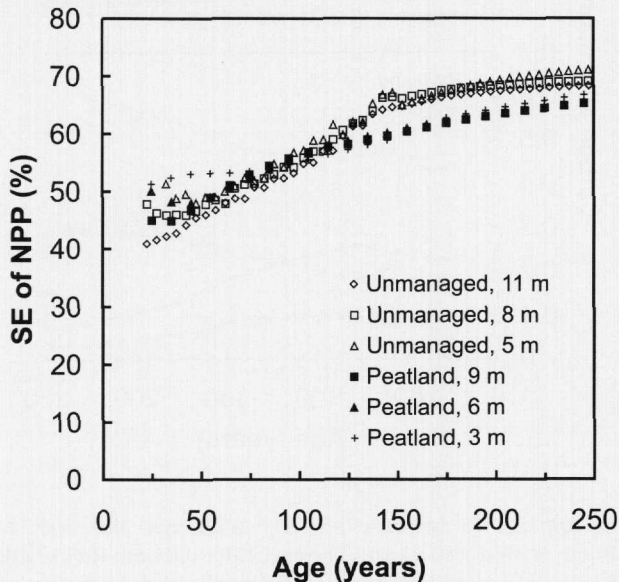
for the static components. Because the relative contribution of biomass components (e.g., stemwood, foliage) to the total biomass growth rate changes with age and SI, the SE value of total biomass growth varies with age and SI as well, with an average value of 26%.

Based on the foliage and branch turnover rates measured by Gower et al. (1997) in Saskatchewan and Manitoba, SE for litterfall could be as high as 70%. With the fine-root turnover rates varying by as much as 33% of the mean (Steele et al. 1997; Gower et al. 1997), SE of total fine-root production is 76%. From section 2.3, the SE for mortality is 23.5%. For understory vegetation, aboveground NPP of 23–60 g C·m^{-2}·year^{-1} used in the current study compares well with the Canada-wide values of 16–60 g C·m^{-2}·year^{-1} reported by Weetman and Timmer (1967). Hence, we assume that SE of understory aboveground NPP is approximately 50%.

With all of these estimation errors considered, the SE of our estimates of stand NPP range from 40 to 70%, with a mean of about 60% (Fig. 9). The SE is lower in the early stages of development, because total NPP is dominated by growth of biomass components that can be estimated with a comparatively low SE. As stands develop, however, NPP becomes increasingly dominated by fine-root turnover and litterfall, both of which have larger SEs. To improve the accuracy of these NPP estimates, more accurate measurements

of fine-root biomass, fine-root turnover rate, foliage biomass, and needle life-span along chronosequences and SI gradients would be required. With the advances in optical measurement of leaf area (Chen et al. 1997), litterfall traps, and use of minirhizotrons for estimating fine-root production (Steele et al. 1997; Gower et al. 1997), such measurements are possible and should be pursued.

Another error in the age–NPP relationships may arise from errors inherent in the yield tables. In addition to age and SI, the values reported in yield tables (e.g., *H*, *D*, and *V*) are also affected by sample sizes, site locations, environmental variability, and stand density. Noting that the mean actual heights at 50 years reported for peatland SI = 9 (8.6 m) and for unmanaged SI = 8 (8.2 m) were similar, we used them to evaluate the error that could be caused by different yield tables. If we use unmanaged SI = 8 to represent peatland SI = 9, the estimated NPP is 0–14% greater. To evaluate the effect of variable densities on estimated NPP, we applied the black spruce yield tables developed by Evert (1970) for the Ontario Clay Belt. For 30 years < *A* < 120 years and SI = 9, NPP of the fully stocked stands was estimated to be 2–18% higher than that of a stand with 50% stocking. Not surprisingly, the differences were greatest for the youngest stands but diminished with age as the half-stocked stands reached full site occupancy (i.e., before competition imposed a constraint on stand growth).

Because of the possibility that some of these estimation errors may cancel each other, the SE determined here are likely to be the upper limits for the estimates of NPP. Comparison with NPP measurements reported by Gower et al. (1997) in Saskatchewan and Manitoba, by Ruess et al. (1996) in Alaska, and by Grigal et al. (1985) in Minnesota indicates that NPP estimated using the current method agrees with these measurements to within ±25% (Table 1). It is likely that the latter measurements were affected by climate variability, whereas, as mentioned previously, the yield table data are "smoothed" over many years of observations. This suggests that the estimates of NPP derived from yield tables could actually be more accurate indicators of long-term productivity than direct measurements made over short periods. Hence, the general agreement indicates that our yield table based method will provide a reasonable first approximation of stand-level NPP. Based on this approximation, more accurate estimation can be made when the effects of environmental variability are incorporated.

5. Concluding remarks

We have developed a practical method for estimating mean age–NPP relationships from available stand yield ta-

bles, biomass equations, and turnover data for fine roots and foliage. This method is similar in principle to that of Gower et al. (1997) and Bernier et al. (1999), who estimated stand-level NPP in a specific year using measured annual radial increment, biomass allometric equations, and measured foliage and root turnover rates. Our method differs, however, in that yield table data are used in place of measured annual radial increment, so that changes in NPP with age can also be estimated. Since yield tables represent average growth rates for a given site index, the age–NPP relationships derived in this study do not account for interannual climate variability. The effect of interannual climate variability on NPP can be estimated using physiological models (e.g., Peng and Apps 1999; J.M Chen et al. 2000; W.J. Chen et al. 2000a, 2000b).

Applying this method, we developed systematic mean age–NPP relationships for black spruce stands in Ontario. As expected from consideration of yield curves for even-aged stands, higher productivity stands achieve maximum NPP earlier than less productive stands. In our analysis, maximum NPP was estimated to be ~400 g $C \cdot m^{-2} \cdot year^{-1}$ at about 40 years for the most productive unmanaged stand (SI = 11 m), while the least productive peatland stand (SI = 3 m) achieved a maximum NPP of ~230 g $C \cdot m^{-2} \cdot year^{-1}$ at around 160 years. The decrease in NPP with age was also more dramatic for higher productivity sites.

An analysis of the separate components of above- and below-ground NPP indicated that decrease in the growth of woody tissues is the main contributor to the decline in NPP with age.

Carbon allocation coefficients were also shown to vary with age and SI, instead of being constant as is often assumed in many forest C budget models. As expected, our analysis showed that C allocation to woody components (stems, branches, and coarse roots) was higher on more productive sites, whereas a greater proportion of available NPP is allocated to fine roots and foliage in lower productivity stands. The more productive stands are also characterized by relatively rapid decreases in C allocation to woody components with increasing age.

Based on error assessment for various components, we estimated that the SE of estimation for NPP increases with age from 40 to 70%, with a mean of 60%. The error attributable to factors such as environmental variability and differences in stand density, was estimated to be as large as 20%. Comparison with NPP measurements reported by Gower et al. (1997) in Saskatchewan and Manitoba, by Ruess et al. (1996) in Alaska, and by Grigal et al. (1985) in Minnesota indicates NPP estimated using this method agree with observations to within ±25%.

Fine-root turnover and litterfall are the two most uncertain components in the stand-level estimates of NPP. Hence, the accuracy of NPP estimated using this yield-table based method could be substantially improved, if more data were available. We feel that comprehensive site-level quantification of fine-root biomass, fine-root turnover, and of leaf production and turnover should be carried out for forest ecosystems across Canada, as a matter of urgency.

Acknowledgements

References

Alemdag, I.S. 1983. Mass equations and merchantability factors for Ontario softwoods. Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. PI-X-23.

Bernier, P.Y., Fournier, R., Ung, C.H., Robitaille, G., Larocque, G., Lavigne, M.B., Boutin, R., Raulier, F., Paré, D., Beaubien, J., and Delisle, C. 1999. Linking ecophysiology and forest productivity: an overview of the ECOLEAP project. For. Chron. 75: 417–421.

Cannell, M.G.R. 1982. World forest biomass and primary production data. Academic Press, London, New York.

Chen, J.M., Rich, P.M., Gower, S.T., Norman, J.M., and Plummer, S. 1997. Leaf area index of boreal forests: theory, techniques, and measurements. J. Geophys. Res. 102: 29 429 – 29 443.

Chen, J.M., Chen, W.J., Liu, J., Cihlar, J., and Gray, S. 2000. Annual carbon balance of Canada's forest during 1895–1996. Global Biogeochem. Cycles, 14: 839–850.

Chen, W.J., Chen, J.M., and Cihlar, J. 2000a. An integrated terrestrial carbon-budget model based on changes in disturbance, climate, and atmospheric chemistry. Ecol. Modell. 135: 55–79.

Chen, W.J., Chen, J.M., Liu, J., and Cihlar, J. 2000b. Approaches for reducing uncertainties in regional forest carbon balance. Global Biogeochem. Cycles, 14: 827–838.

Evert, F. 1970. Black spruce growth and yield at various densities in the Ontario Clay Belt. For. Sci. 16: 183–195.

Evert, F. 1985. Systems of equations for estimating ovendry mass of 18 Canadian tree species. Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. PI-X-59.

Finer, L., Messier, C., and Grandpré, L. 1997. Fine root dynamics in mixed boreal conifer – broad-leafed forest stands at different successional stages after fire. Can. J. For. Res. 27: 304–314.

Friedlingstein, P., Joel, G., Field, C.B., and Fung, I.Y. 1999. Toward an allocation scheme for global terrestrial carbon models. Global Change Biol. 5: 755–770.

Frolking, S. 1997. Sensitivity of spruce/moss boreal forest net ecosystem productivity to seasonal anomalies in weather. J. Geophys. Res. 102(D24): 29 053 – 29 064.

Gonzalez, J.S. 1990. Wood density of Canadian tree species. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-315.

Gower, S.T., McMurtrie, R.E., and Murty, D. 1996. Aboveground net primary production decline with stand age: potential causes. Trees, 11: 378–382.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., and Stow, T.K. 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(D24): 29 029 – 29 041.

Grigal, D.F., Buttleman, C.G., and Kernik, L.K. 1985. Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Can. J. Bot. 63: 2416–2424.

Hall, J.P. 1984. The relationship between wood density and growth rate and the implications for the selection of black spruce plus trees. Can. For. Serv. Nfld. For. Res. Cent. Inf. Rep. N-X-224.

Halliwell, D.H., and Apps, M.J. 1997. Boreal Ecosystem–Atmosphere Study (BOREAS) biometry and auxiliary sites: overstory and understory data. Canadian Forestry Service, Northern Forest Centre, Edmonton, Alta.

Hendrick, R.L., and Pregitzer, K.S. 1993. Patterns of fine root mortality in two sugar maple forests. Nature (London), **361**: 59–61.

Houghton, J.T., Meira, L.G., Callander, B.A., Harries, N., Kattenberg, A., and Maskell, K. (*Editors*). 1996. Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, U.K.

Hunt, E.R., Lavigne, M.B., and Franklin, S.E. 2000. Factors controlling the decline of net primary production with stand age for balsam fir in Newfoundland assessed using an ecosystem simulation model. Ecol. Modell. **122**: 151–164.

Ker, M.F. 1984. Biomass equations for seven major Maritimes tree species. Can. For. Serv. Maritimes For. Cent. Inf. Rep. M-X-148.

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.

Kurz, W.A., Apps, M.J., Webb, T.M., and McNamee, P.J. 1992. The carbon budget of the Canadian forest sector: phase I. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-326.

Kurz, W.A., Beukema, S.J., and Apps, M.J. 1996. Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector. Can. J. For. Res. **26**: 1973–1979.

Lavigne, M.B. 1982. Tree mass equations for common species of Newfoundland. Can. For. Serv. Nfld. For. Cent. Inf. Rep. N-X-213.

Liu, J., Chen, J.M., Cihlar, J., and Chen, W.J. 1999. Net primary productivity distribution in the BOREAS study region. J. Geophys. Res. **104**(D22): 27 735 – 27 754.

Malik, V., and Timmer, V.R. 1998. Biomass partitioning and nitrogen retranslocation in black spruce seedlings on competitive mixedwood sites: a bioassay study. Can. J. For. Res. **28**: 206–215.

Manning, G.H., Massie, M.R.C., and Rudd, J. 1984. Metric single-tree weight table for the Yukon Territory. Can. For. Serv. Pacific For. Cent. Inf. Rep. BC-X-250.

McGuire, A.D., Melillo, J.M., Kicklighter, D.W., Grace, A.L., Moore, B., III, and Vorosmarty, C.J. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochem. Cycles, **6**: 101–124.

Murty, D., McMurtrie, R.E., and Ryan, M.G. 1996. Declining forest productivity in aging forest stands: a modeling analysis of alternative hypotheses. Tree Physiol. **16**: 187–200.

Nadelhoffer, K.J., and Raich, J.W. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology, **73**: 1139–1147.

Payandeh, B. 1990. Preliminary yield functions and tables for peatland black spruce in Ontario. Can. For. Serv. Great Lakes For. Cent. Inf. Rep. O-X-405.

Peng, C.H., and Apps, M.J. 1999. Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. Ecol. Modell. **122**: 175–193.

Perry, D.A. 1994. Forest ecosystems. Johns Hopkins Press Ltd., London.

Plonski, W.L. 1981. Normal yield tables (metric) for major forest species of Ontario. Ontario Ministry of Natural Resources, Sault Ste. Marie, Ont.

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

Publicover, D.A., and Vogt, K.A. 1993. A comparison of methods for estimating fine root production with respect to sources of error. Can. J. For. Res. **23**: 1179–1186.

Rapalee, G., Trumbore, S.E., Davidson, E.A., Harden, J.W., and Veldhuis, H. 1998. Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. Global Biogeochem. Cycles, **12**: 687–701.

Rastetter, E.B., Agren, G.I., and Shaver, G.R. 1997. Response of N-limited ecosystems to increased CO_2: a balanced-nutrition, coupled-element-cycle model. Ecol. Appl. **7**: 444–460.

Reich, P.B., Kioke, T, Gower, S.T., and Schoettle, A.W. 1995. Causes and consequences of variation in conifer leaf life-span. *In* Ecophysiology of coniferous forests. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, Calif. pp. 225–254.

Ruark, G.A., and Bockheim, J.G. 1988. Biomass, net primary production, and nutrient distribution for an age sequence of *Populus tremuloides* ecosystems. Can. J. For. Res. **18**: 435–443.

Ruess, R.W., van Cleve, K., Yarie, J., and Viereck, L.A. 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can. J. For. Res. **26**: 1326–1336.

Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27. pp. 213–261.

Singh, T. 1984. Biomass equations for six major tree species of the Northwest Territories. Can. For. Serv. North. For. Cent. Inf. Rep. Nor-X-257.

Singh, T. 1986. Wood density variation of six major tree species of Northwest Territories. Can. J. For. Res. **16**: 127–129.

Smith, F.K., and Long, J.N. 2001. Age-related decline in forest growth: an emergent property. For. Ecol. Manage. **144**: 175–181.

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

Steele, S.J., Gower, S.T., Vogel, J.G., and Norman, J.M. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. **17**: 577–587.

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.

Weetman, G.F., and Timmer, V. 1967. Feather moss growth and nutrient content under upland black spruce. Pulp and Paper Research Institute of Canada, Pointe-Claire, Que. Tech. Rep. 503.

Würth, G., Häger, C., and Kohlmaier, G.H. 1997. The Frankfurt biosphere model (FBM): regional validation using German forest yield tables and inventory data and extrapolation to a $2\times CO_2$ climate. *In* Carbon dioxide mitigation in forestry and wood industry. *Edited by* G.H. Kohlmaier, M. Weber, and R.A. Houghton. Springer-Verlag, Heidelberg. pp. 293–321.