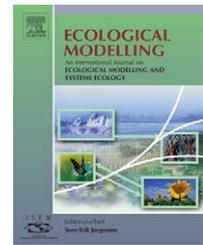


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/ecolmodel

Formulating and parameterizing the allocation of net primary productivity for modeling overmature stands in boreal forest ecosystems

Xiaolu Zhou^{a,b}, Changhui Peng^{a,*}, Qing-Lai Dang^b

^a Institut des sciences de l'environnement, Département des sciences biologiques, Université du Québec à Montréal, Case postale 8888, Succursale Centre-Ville, Montréal, Canada, H3C 3P8

^b Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, Canada, ON P7B 5E1

ARTICLE INFO

Article history:

Received 21 December 2004

Received in revised form 24 October 2005

Accepted 15 November 2005

Published on line 28 December 2005

Keywords:

Carbon allocation

Dynamic NPP allocation

Process-based model

Ecosystem modelling

Black spruce

ABSTRACT

In process-based models of forest ecosystems, carbon allocation is a key process that partitions the net primary productivity (NPP) among different biomass components and thus affects forest growth patterns at different stages of the forest's growth. Common allocation models usually express the carbon allocation as linear or monotonic functions of time. These models are acceptable for a limited growth period, but inadequate for simulating long-term development of a forest. To improve the usefulness of these models and simplify the model structure, we developed an analytical solution to partition NPP that considers the effects of litterfall and growth rate. We derived NPP allocation functions based on functions for the net growth rate (dry mass) and based on empirical growth curves estimated from normal yield tables for northern Ontario, Canada. The improved allocation reflects growth restrictions that arise in overmature stands according to different site classes across landscape. The details of the derivation and parameterization are presented and discussed. We validated the new NPP allocation functions for black spruce (*Picea mariana*) in the boreal forest of northern Ontario. The improved NPP allocation simulated the NPP dynamics of forest ecosystems more accurately over the course of stand development, and the results were biologically realistic.

© 2005 Elsevier B.V. All rights reserved.

1. Introduction

In most process-based forest ecosystem models, carbon allocation is a key process, and the gross primary productivity (GPP) derived from leaf photosynthesis is divided among metabolic processes such as respiration and net primary productivity (NPP). NPP is then partitioned between litterfall and the structural material that comprises three main biomass components (stem, roots, and foliage). As a result of currently limited knowledge of the internal processes that govern this partitioning, the mechanisms that determine the amount of

carbon allocated to any part of a tree are not well understood (Cannell and Dewar, 1994; Landsberg and Waring, 1997). The resulting uncertainty in modeling of carbon allocation makes it difficult to simulate the carbon acquisition and growth patterns of trees and to estimate litterfall and fine root turnover. This presents a big challenge in the development of models for simulating the carbon dynamics of forest ecosystems.

Since the late 1980s, a number of ecological models, including both process-based and hybrid models, have been developed for simulating ecosystem processes and the development of forest stands. Existing approaches to NPP allocation

* Corresponding author. Tel.: +1 514 987 3000x1056; fax: +1 514 987 4718.

E-mail address: peng.changhui@uqam.ca (C. Peng).

0304-3800/\$ – see front matter © 2005 Elsevier B.V. All rights reserved.

doi:10.1016/j.ecolmodel.2005.11.022

fall into three main categories: (1) mechanistic models (e.g., TREGRO: Weinstein et al., 1991; FIWALD: Schall, 1991; TREE-DYN3: Bossel, 1996) specialize in using priorities in phenology and nutrient status to govern NPP allocation (Tiktak and Grinsven, 1995). They usually assume that, for example, respiration needs must be satisfied first, and only then is carbon allocated in turn to leaves, fine roots, fruits, and stems. The carbon allocation is considered to be affected by nutrient levels during the growth period, but not by biological and environmental restrictions that change as a function of tree age. (2) Empirical functions depend on the tree's age or diameter at breast high (DBH) (e.g., FOREST-BGC: Running and Coughlan, 1988; FAGUS: Hoffmann, 1995; 3-PG: Landsberg and Waring, 1997; NITGRO: Battaglia et al., 1999; CenW: Kirschbaum, 1999; ASPECTS: Rasse et al., 2001). The NPP allocation is calculated based on age or DBH using empirical parameters, allometric relationships, and trend lines. (3) Empirical constants are used to define allocation ratios (e.g., Century 4.0: Parton et al., 1993; NICCCE: van Dam and van Breemen, 1995; SIMA: Kollomäki, 1998; SIERRA: Mouillot et al., 2001). Generally speaking, the empirical functions have been widely developed and used based on how allocation is affected by growth conditions. Many these models have been successfully used to simulate stand development and have captured the actual status of NPP allocation in a stand. However, the parameters of the NPP allocation functions have reflected only empirical estimates for specific locations, and there was no methodology that could parameterize the functions so they could be adapted to different forest ecosystems. The allocation functions also did not interpret the dynamics of NPP allocation in tree growth for overmature forests. They are thus inadequate for simulating long-term development of a forest ecosystem.

The object of the present study was to develop a general approach for partitioning NPP when simulating overmature stands in the boreal forest ecosystems of Canada. We present an analytical solution that expresses the dynamic aspects of NPP allocation. The NPP allocation functions were derived based on the net rates of dry mass production and on empirical growth curves such as the normal yield tables developed by Plonski (1974). These functions improved the empirical NPP allocation models described above, and reflected the growth restrictions that occur in overmature stands for various species and site classes. The details of the derivation and parameterization of these functions is presented. We also validated the NPP allocation functions using data for black spruce (*Picea mariana*) in the boreal forest of northeastern Ontario, Canada.

2. Methods

2.1. NPP allocation functions

In the processes responsible for NPP allocation, different partitions affect the growth patterns of each tree component and the final results of the NPP simulation during different periods of the tree's life. As a broadly accepted empirical function, NPP allocation is primarily constructed based on two assumptions: first, carbon allocation can be estimated using allocation coefficients, as shown in Eq. (1) (McMurtrie and Landsberg, 1992).

Table 1 – Symbols used for formulating the NPP allocation functions

Name	Unit	Note
η_{coarse}		Allocation coefficient for coarse roots
η_f		Allocation coefficient for foliage
η_{fine}		Allocation coefficient for fine roots
η_r		Allocation coefficient for roots (total coarse and fine roots)
η_s		Allocation coefficient for the stem
A	kg	Maximum of individual stem biomass
a_f and b_f		Genetic characteristics of different tree species for foliage
a_r and b_r		Genetic characteristics of different tree species for roots
a_s and b_s		Genetic characteristics of different tree species for the stem
b		Coefficient expressing initial stem biomass
c_r		Coefficient to reflect the relation of $r_{f\text{max}}$ and r_{f0}
D	mm	DBH
h	t C m^{-3}	The carbon density of wood
k		Time coefficient for the stem biomass growth function
k_f		Time coefficient for the foliage loss function (r_f) that ranges from r_{f0} to $r_{f\text{max}}$
M		Nutrient coefficient
m		Allometric constant reflecting assimilation rate
N	kg	Net primary production of a tree
p		Coefficient of anabolism or assimilation
$Q_{\text{root_stem}}$		Ratio of the coarse root (η_{coarse}) to stem (η_s) allocation coefficients
$Q_{\text{root_foliage}}$		Ratio of the fine root (η_{fine}) to foliage (η_f) allocation coefficients
Q		Ratio of the foliage (η_f) to stem (η_s) allocation coefficients
Q'		Simplified Q
q		Coefficient of catabolism or dissimulation
r_f		Rate of foliage loss per year
$r_{f\text{max}}$		Maximum foliage litterfall (including twigs and small branches) per year
r_{f0}		Foliage loss per year when $t=0$
r_r		Loss of roots per year
r_s		Loss of stem per year
t	Year	Time in years
v_{max}	m^3	Maximum of individual tree volume
W	kg	Total mass of the tree
w_f	kg	Mass of foliage
w_r	kg	Mass of roots
w_s	kg	Mass of stem
α_f and β_f		Coefficients instead of a_f and b_f
α_s and β_s		Coefficients instead of a_s and b_s

Second, allometric relationships between each part of the tree and total tree biomass can be described as in Eq. (2) for individual trees (Pearson et al., 1984), and these relationships often fit the observed data well (i.e., with high R^2 values):

$$\sum \eta_i = 1 \quad (i = f, r, s) \tag{1}$$

$$w_i = a_i W^{b_i} \quad (i = f, r, s) \tag{2}$$

where the parameters and symbols used for formulating the NPP allocation functions are summarized in Table 1.

To simplify our problem analysis, we did not consider carbon allocations to bark, pollen, and fruit in this study. We also defined branches as a part of the stem, but included lost branches and twigs in the foliage litterfall. Each of the allocation coefficients in Eq. (1) can be derived from the growth functions of NPP. *McMurtrie and Wolf (1983)* presented growth functions in differential form, and expressed the rate of growth in the mass of foliage (w_f), roots (w_r), and stem (w_s) as follows:

$$\frac{dw_f}{dt} = \frac{dN}{dt} \eta_f - r_f w_f \tag{3}$$

$$\frac{dw_r}{dt} = \frac{dN}{dt} \eta_r - r_r w_r \tag{4}$$

$$\frac{dw_s}{dt} = \frac{dN}{dt} \eta_s - r_s w_s \tag{5}$$

If we assume that $r_s = 0$ for a single tree, we can derive Eq. (6) from Eqs. (3) and (5):

$$\frac{\eta_f}{\eta_s} = \left(\frac{dw_f}{dt} \right) \left(\frac{dw_s}{dt} \right)^{-1} + r_f w_f \left(\frac{dw_s}{dt} \right)^{-1} \tag{6}$$

If we express the ratio η_f/η_s as Q and incorporate this new term in Eq. (6):

$$Q = Q' + r_f w_f \left(\frac{dw_s}{dt} \right)^{-1} \tag{7}$$

$$\text{where } Q' = \left(\frac{dw_f}{dt} \right) \left(\frac{dw_s}{dt} \right)^{-1} \tag{8}$$

If we disregard the term $r_f w_f (dw_s/dt)^{-1}$ in Eq. (7), the Q' term approximates the ratio of η_f and η_s for some species or younger trees that have a low foliage litterfall rate or low foliar biomass; under these conditions, $r_f w_f (dw_s/dt)^{-1}$ becomes small enough to ignore. If we substitute Eq. (2) into Eq. (8), then differentiate w_f and w_s , we obtain the following result:

$$Q' = (a_f b_f) (a_s b_s)^{-1} (W^{b_f - b_s}) \tag{9}$$

Then, from Eq. (1):

$$\eta_s = (1 - \eta_r)(Q' + 1)^{-1} \tag{10}$$

$$\eta_f = 1 - \eta_r - \eta_s \tag{11}$$

where $Q' \approx \eta_f/\eta_s$. Eqs. (9)–(11) have been used in the 3-PG model (*Landsberg and Waring, 1997*), which allocates carbon to roots (η_r) directly as a function of a nutrient coefficient (M), absorbed photosynthetically active radiation (PAR), and utilizable photosynthetically active radiation (UPAR):

$$\eta_r = 0.8 \left[1 + 2.5M \left(\frac{UPAR}{PAR} \right) \right]^{-1} \tag{12}$$

Fig. 1a illustrates an example of the NPP allocation coefficients using Q' instead of Q . Note that the graphs in this figure are presented based on data for site class 1 black spruce in northern Ontario (**Table 2**), with tree ages estimated from DBH using

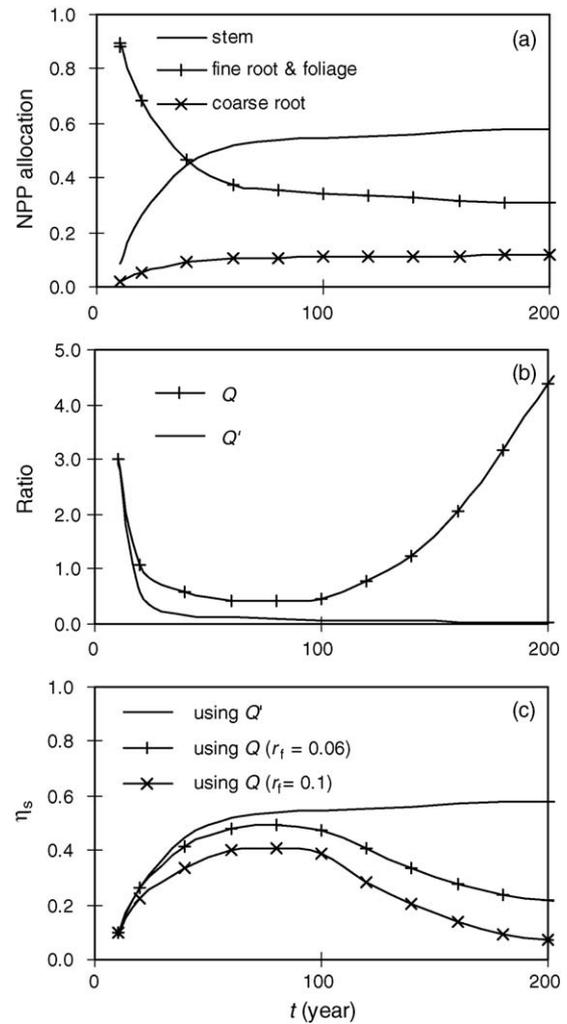


Fig. 1 – Comparisons of NPP allocation using the allocation ratios Q and Q' (see the text for definitions of these ratios) as a function of the tree’s age (t). (a) NPP allocation using Q' ; (b) comparison of Q and Q' ; (c) comparison of NPP allocation between different allocation ratios (Q and Q') and different foliage loss rates (r_f). This comparison is based on data for black spruce (site class = 1; **Table 2) in northern Ontario, and tree ages estimated from DBH using a normal yield table for this species (*Plonski, 1974*). Q' was calculated using Eq. (A1.11).**

a normal yield table for this species (*Plonski, 1974*). In this figure, η_s is an increasing monotonic function of time, and as it increases, partitioning to fine roots and foliage decreases. However, NPP should logically be increasingly allocated to roots and foliage as an overmature tree gradually decreases its stem growth. This suggests that the coefficients for carbon allocation estimated using Q' do not describe the actual pattern of NPP allocation in older trees as a result of omitting the $r_f w_f (dw_s/dt)^{-1}$ term in Eq. (9). This term can be interpreted as the ratio of foliar turnover to growth rate of stem mass. Once the values of foliar turnover and stem increment become comparable, which is the case for older trees, their ratio can no

Table 2 – Parameters used in Eq. (13) for black spruce. The parameters α_f and β_f , determined by analyzing field data (Newcomer et al., 2000)

Site class	r_{fmax}	r_{fo}	k_r	α_f	β_f	α_s	β_s	v_{max}	k
1	0.1	0.01	0.12	0.00119	1.71705	0.000023	2.9736	0.330	0.0464
2	0.1	0.01	0.12	0.00119	1.71705	0.000052	2.8189	0.189	0.0423
3	0.1	0.01	0.12	0.00119	1.71705	0.000077	2.7052	0.010	0.0442

Parameters α_s , β_s , v_{max} , and k were obtained from regression curves developed using normal yield tables (Plonski, 1974). The maximum rate (r_{fmax}) of foliage litterfall, including twigs, was calculated from field measurements (Gower et al., 1997). Site classes were classified using the normal yield tables (Plonski, 1974) for the boreal forest of northern Ontario, Canada. Site classes 1, 2, and 3 represent high, medium, and low site productivity, respectively. Note that Eq. (13) includes the following functions: $r_f = r_{fmax}(1 + c_r e^{-krt})^{-1}$ and $c_r = 1 - r_{fmax}r_{fo}^{-1}$.

longer be ignored. Thus, the following derivation accounts for the $r_f w_f (dw_s/dt)^{-1}$ term in Eq. (7).

Eq. (7) includes four subfunctions of time (t): Q' , w_f , r_f , and dw_s/dt . The first three of these subfunctions are (respectively) decreasing monotonic (Q'), increasing monotonic (w_f), and unchanging (r_f). All three terms become nearly constants when tree age or DBH becomes sufficiently large. Therefore, the term that describes the growth rate of the stem (dw_s/dt) in Eq. (9) significantly affects the curve for Q at high values of age or DBH. To simplify the problem and facilitate data collection, we integrated dw_s/dt and expressed Q using DBH (D) as an independent variable:

$$Q = (\alpha_f \beta_f)(\alpha_s \beta_s)^{-1} (D^{\beta_f - \beta_s}) + k r_f \alpha_f \alpha_s D^{\beta_f - \beta_s} \times [1 - \alpha_s D^{\beta_s} (2000 h v_{max})^{-1}]^{-1} \tag{13}$$

The derivation of Eq. (13) is described in more detail in Appendix A. The function Q can be parameterized using field data for simulations of tree growth on different sites. Fig. 1b illustrates an example of curves for Q and Q' , and Fig. 1c shows the different effects of Q and Q' to NPP allocation (η_s), where both Q and Q' were calculated based on determining parameter k in Eq. (A1.2), α_i and β_i ($i = f, s$) in Eq. (A1.6), h and v_{max} in Eq. (A1.9), and r_f in Eq. (3).

2.2. Parameterization

The parameters α_f and β_f in the allometric relationships between foliage biomass and DBH were determined by regression analysis of field data (Newcomer et al., 2000) collected from black spruce sites in the BOREAS (Sellers et al., 1997) of the boreal forest ecosystems of central Canada, which consists of a northern study area (NSA) near Thompson, Manitoba (55.7°N, 97.8°W) and a southern study area (SSA) near Prince Albert, Saskatchewan (53.2°N, 105.7°W). The regression function for foliage ($w_f = 0.00119D^{1.171705}$) had a good correlation ($R^2 = 0.90$, $n = 116$) for black spruce.

The parameters α_s and β_s in the allometric relationships between stem biomass and DBH were calculated by means of regression analysis of the volume data in normal yield tables for black spruce in northern Ontario. The total volume (m^3) was converted into biomass (kg) using a carbon density factor ($h = 0.23 \text{ t C m}^{-3}$; Zhou et al., 2004) and a ratio of carbon to total biomass equal to 0.5 (Environment Canada, 2004), which was also used for determining the parameters A and k those describe the relationship between stem biomass and tree age.

In this study, we used a litterfall function (Landsberg and Waring, 1997) for calculating the foliage loss rate as $r_f = r_{fmax} (1 + c_r e^{-krt})^{-1}$ and $c_r = 1 - r_{fmax}r_{fo}^{-1}$. We assumed that $r_{fo} = 0.01 \text{ year}^{-1}$ and $k_r = 0.12$, as was suggested in the 3-PG model (Landsberg and Waring, 1997), and set $r_{fmax} = 0.10 \text{ year}^{-1}$, which combines the fine branch and foliage litterfall rates measured by Gower et al. (1997): fine branch = 0.024 year^{-1} , and foliage = $0.069 - 0.083 \text{ year}^{-1}$ and $0.061 - 0.075 \text{ year}^{-1}$ for SSA and NSA, respectively. The value of r_f ranges from 0.01 to 0.10 year^{-1} and approaches r_{fmax} when $t > 30$ months (approximately). Table 2 lists all parameters described in Eq. (13) and their values.

For practical use, we simplified Eq. (10) as Eq. (14) using empirical ratios instead of Eq. (12), and expressed it using a single independent variable (Q) for Canada's boreal forest:

$$\eta_s = (1.2 + 3Q)^{-1} \tag{14}$$

The expression of η_s was derived as Eq. (A2.4) as described in Appendix B. The ratio $Q_{\text{croot.stem}}$ (0.2 for black spruce) was calculated from measurements in the BOREAS study areas (NSA and SSA) in central Canada (Gower et al., 1997; Ryan et al., 1997). The ratio $Q_{\text{froot.foliage}}$ (2.0) was estimated from Ryan et al., (1997). Substituting these values of $Q_{\text{croot.stem}}$ and $Q_{\text{froot.foliage}}$ into Eq. (A2.4), we obtained Eq. (14) and solved for η_f and η_r using $Q = \eta_f/\eta_s$ and Eq. (1).

2.3. Model validation

We used the TRIPLEX1.0 (Peng et al., 2002) simulation model as the candidate for testing the new NPP allocation functions. This model simulates the key variables of the carbon cycle in an ecosystem, such as PAR, GPP, NPP allocation, forest growth and yield, soil carbon, soil nitrogen, and soil water. The variables for tree growth and yield were calculated based on a function that describes the stem's wood biomass increment. Tree height and diameter growth are both influenced by a combination of physiological and morphological responses to environmental factors. This provides a way to validate the process-based model using field growth and yield data. We integrated Q and Q' into TRIPLEX1.0 for partitioning NPP, and compared the simulated height and DBH results with field data to obtain an indirect validation of the stem allocation coefficient (η_s) in this study. TRIPLEX1.0 has been parameterized for major boreal tree species in central Canada (Zhou et al., 2004).

The TRIPLEX1.0 model requires inputs of forest stand data, soil texture, and climatic conditions before it can simulate a

stand. We obtained field growth and yield data for the model simulation from the Lake Abitibi Model Forest (LAMF) of north-eastern Ontario (48.8°N, 80.7°W). The vegetation data from the 1993 Iroquois Falls Forest Inventory was provided by the Abitibi-Consolidated Company of Canada. Black spruce covered more than 75% of the LAMF area, and average tree age ranged from 2 to 280 years in 1993. Annual average temperature was 1.6 °C and annual precipitation was 976 mm at central LAMF (Iroquois Falls) in 1990 (Environment Canada, 1994). Data on soil texture were reported by Elkie et al. (2000) and Siltanen et al. (1997). The average temperature, humidity and precipitation for whole LAMF region were obtained from the climate database developed by Canadian Centre for Climate Modelling and Analysis (CCCMA, 2003).

3. Results

The analytical functions for NPP allocation that we developed in this study are expressed by Eqs. (13) and (14), and are graphed as Fig. 2. The NPP allocation to stem decreases obviously after 100 years, and differs among site classes. All the parameters listed in Table 2 were used in this study to simulate the growth of black spruce in northeastern Ontario's boreal forest.

In Eq. (14), the ratio of foliage to stem allocation (Q) increases as the trees age, and this decreases the stem allocation coefficient (η_s) in older age classes. If D reaches its maximum value in Eq. (13) and meets the condition $\alpha_s D^{\beta_s} \leq 2000h\nu_{\max}$, then Q tends to increase to ∞ and η_s becomes zero. For instance, when $D_{\max} = 196.5$, $\nu_{\max} = 0.33$, and $h = 0.23$, the second term in Eq. (13) approaches infinity, which results in a zero allocation of NPP to the stem. Fig. 1b compares Q and Q' as a function of time (years), with these values calculated from DBH using the data in normal yield tables for black spruce. The difference between Q and Q' is obvious when

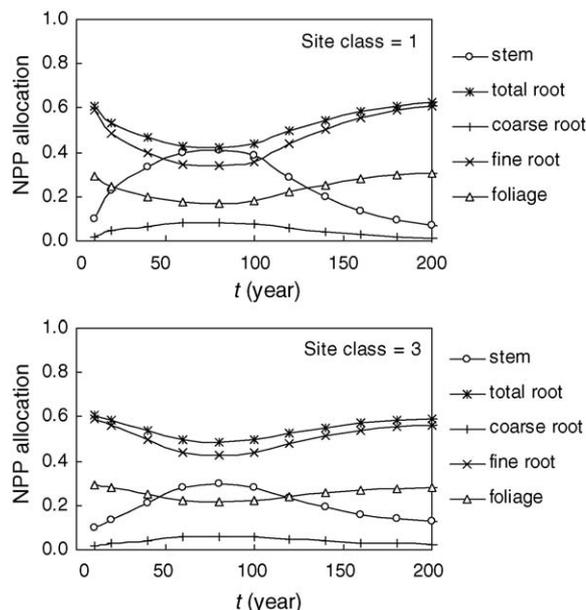


Fig. 2 – An example of NPP allocation curves for black spruce (site classes 1 and 3) in northern Ontario, Canada, calculated from Eqs. (13), (14), (A1.6) and (A2.4) using the parameters in Table 2. Q' was initialized as 3.0 for tree ages of less than 20 years.

trees reach the overmature stage (here, at around 100 years). The increasing Q value results from decreasing η_s as the trees age. Fig. 1c compares the different carbon allocation functions for the stem (η_s) using Q and Q' , and illustrates the effect of the rate of foliage loss (r_f) on η_s . A higher rate (r_f) realistically leads to a lower allocation to the stem (η_s).

The effects on Q and Q' as trees age are obviously different (Fig. 1b). Both the standard errors and the biases estimated

Table 3 – Comparison of \bar{e} , standard errors, standard deviations, and biases for simulated tree height and DBH of black spruce stands using different allocation ratios (Q and Q')

Site class	Height (m)			DBH (cm)		
	1	2	3	1	2	3
<i>n</i>	8184	11783	3999	8184	11783	3999
Using Q'						
\bar{e}	-2.197	-1.668	-0.773	-0.775	-0.825	-0.661
S.E.	1.386	1.925	1.355	1.942	2.472	1.766
S.D.	1.702	2.388	1.520	2.108	2.462	1.875
Bias (%)	-15.6	-13.1	-7.1	-5.3	-5.8	-5.4
<i>p</i> -Value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Using Q						
\bar{e}	-1.351	-0.336	-0.053	0.070	-0.082	-0.153
S.E.	1.374	1.841	1.356	1.939	2.445	1.742
S.D.	1.469	1.933	1.531	1.976	2.216	1.787
Bias (%)	-10.6	-2.7	-0.5	0.5	-0.6	-1.3
<i>p</i> -Value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Note: *n*, sample size (number of stands); \bar{e} , average prediction error; S.E., standard error of the predicted value for each observed value in the regression, which is a measure of the amount of error in the prediction for an individual observation; S.D., standard deviation of the prediction error.

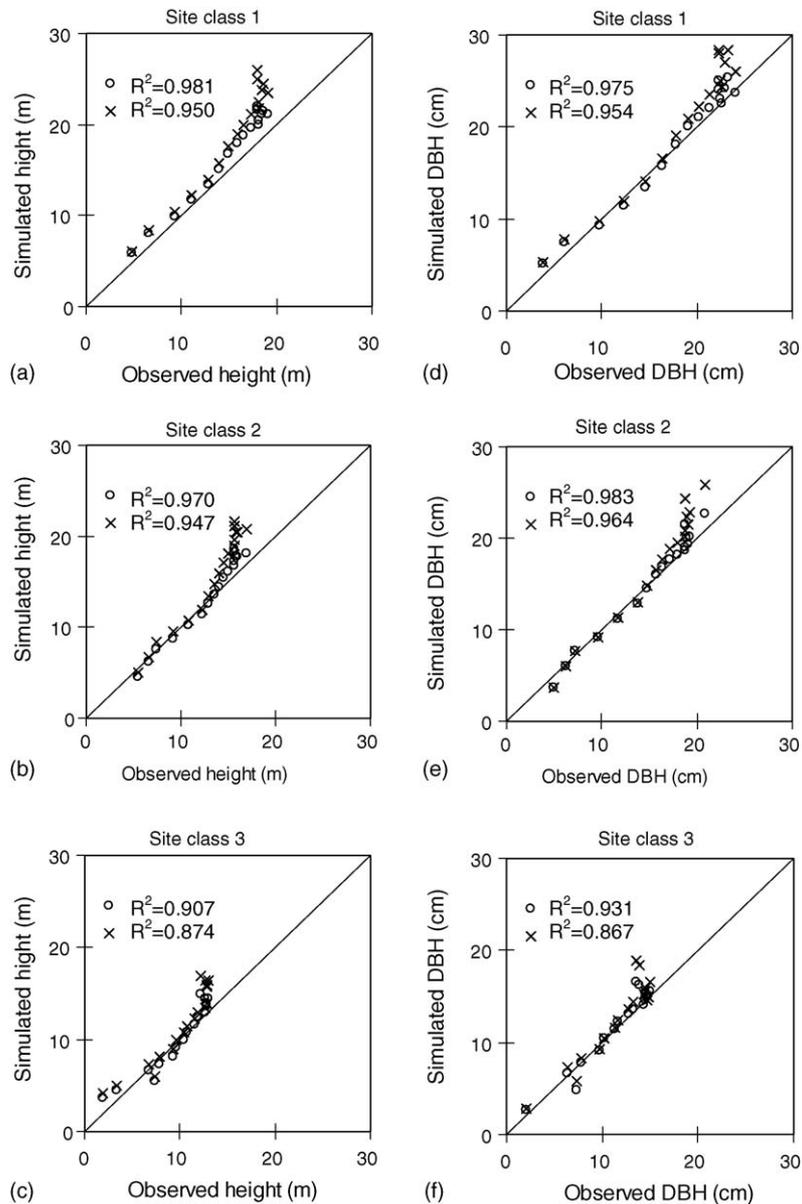


Fig. 3 – Comparison between observed and simulated height and DBH for black spruce using different NPP allocation functions based on two different ratios (i.e., Q and Q'). Field data was collected from the Lake Abitibi Model Forest in northeastern Ontario, Canada. Comparisons between observed and simulated values were performed for each age class. The circle and cross marks denote simulations using Q and Q', respectively. The sample sizes were 8184, 11,783, and 3999 for site classes 1, 2, and 3, respectively.

using Q to predict tree height and DBH are lower than those estimated using Q' for all three site classes (Table 3). The R² correlation between observations and simulations was much higher using Q than using Q' (Fig. 3), and the improved model outputs against the heteroscedasticity error. Fig. 3 also shows differences between the observed and simulated values, especially for older trees with larger DBH and height, since it is realistic to assume that larger DBH and height occur in overmature stands. Table 3 shows that the improved NPP allocation using Q results in less bias than in the traditional NPP allocation using Q' for stands with larger DBH and height.

4. Discussion

Performing a highly accurate simulation is a big challenge for NPP allocation models because many factors affect NPP allocation in a forest ecosystem. From the viewpoint of physiological mechanisms, NPP should be allocated to roots before the stem, and Eq. (10) describes how η_s is affected by η_r . Even though Eq. (12) can be used to calculate η_r by quantifying nutrient and growth conditions, it is awkward to simulate forests over the entire life span of their trees. This problem arises because nutrient transfer and the proportion of usable light (UPAR/PAR)

often exhibit complex long-term behaviors. In Eq. (12), the nutrient coefficient M varies with tree growth and may cause η_r to fluctuate as a function of tree growth with increasing age. If we assume that soil nitrogen accumulates most rapidly between 15 and 64 years after secondary succession following fire or clearcutting (Covington, 1981), M may be higher and may lead η_r to be lower than at other ages. In addition, roots grow fast during the juvenile stage and may thus obtain more NPP allocation. In general, η_r has been estimated as 0.5–0.8 for Sitka spruce (*Picea sitchensis*) (Waring, 2000). This is slightly higher than the range for Canada's boreal black spruce (Chen et al., 2002): 0.4–0.65 for boreal stands (site index of 11 m) and 0.5–0.6 for peatlands (site index of 3 m) in Ontario, Canada.

In this study, we did not provide an analytical value for η_r , but derived an alternative based on estimated and statistical results such as the allocation ratio ($Q_{\text{croot_stem}}$) of coarse roots (η_{coarse}) to stem (η_s), and the allocation ratio ($Q_{\text{froot_foliage}}$) of fine roots (η_{fine}) to foliage (η_f). Fig. 2 illustrates the NPP allocation curves generated in this study. Note that these allocation ratios ($Q_{\text{croot_stem}}$ and $Q_{\text{froot_foliage}}$) were measured and estimated only for a specific location rather than for the whole boreal forest region. This could produce errors in modeling NPP allocation in regions with characteristics that differ from those of central Canada; for example, differences in latitude may also affect the length of fine roots (Hendrick and Pregitzer, 1993). There is thus a need to quantify root allocation ratios for individual species in the boreal forest ecosystem across Canada.

Another problem relates to the parameterization of Eq. (2), which would lead to larger errors for partitioning in younger trees because the power function increases slowly and underestimates biomass when the value of the independent variable (D) is low. In addition, an excessively large biomass may be calculated using Eq. (2) when the value of D becomes higher. For these reasons, we recommend initializing stem biomass and restricting biomass ($\alpha_s D^{\beta_s} \leq A$) before using Eq. (2) and (13). In terms of the effects of latitude on NPP allocation in forests, we also found that the parameters reflecting genetic characteristics in Eq. (2) affect the dynamics of Q , and vary among locations. Using published data (e.g., Aldred and Alemdag, 1988) to fit the parameters used in Eq. (2) for local tree species would improve the accuracy of the model's simulations. Moreover, for practical use of this model, the effects of soil nutrition and moisture needed to be considered as well as complementary effects on NPP allocation.

Generally speaking, Eq. (13) is a DBH-dependent function that interprets the dynamics of NPP allocation to the stem in biological terms. Eqs. (6), (7) and (A1.5) are variations of Eq. (13). They can be used directly to determine allocation to the stem. For example, Q in Eq. (7) can be resolved by calculating the w_f and dw_s/dt (annual increment) values using a process-based model. Fig. 4 compares the different NPP allocation results from four process-based models including 3-PG (Landsberg and Waring, 1997), Century (Parton et al., 1993), CenW (Kirschbaum, 1999), and the present study (an improved version of the TRIPLEX model; Peng et al., 2002). As Fig. 4 shows, NPP allocation to the stem based on the model in the present study decreases obviously during the overmature stage, whereas the other models do not predict this realistic effect because they provide no negative feedback that would

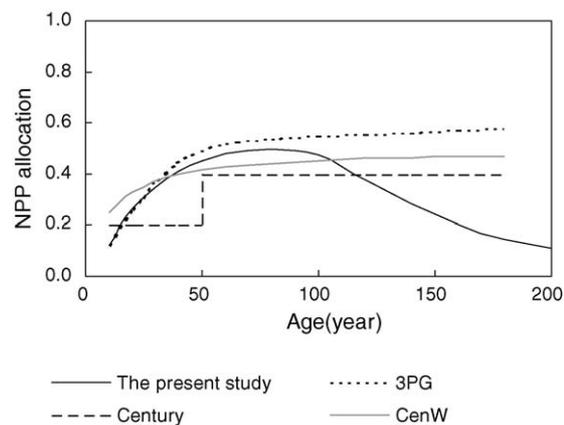


Fig. 4 – Comparisons of simulated NPP allocation to the stem using four different allocation functions derived from different process-based models: the present study, 3-PG (Landsberg and Waring, 1997), Century 4.0 (Parton et al., 1993; Metherell et al., 1993), and CenW (Kirschbaum, 1999). The dynamics of NPP allocation to the stem were simulated over the course of stand development for black spruce, black spruce, common conifer, and Monterey pine, respectively. The Century 4.0 model uses two coefficients to allocate NPP to the stem for both juvenile (<50 years in this study) and mature trees.

constrain the allocation of NPP to the stem. This feedback can be interpreted using the second term in Eq. (13): when DBH (D) reaches its maximum (A), stem growth stops and its allocation becomes zero. Therefore, NPP will be partitioned only to foliage and fine roots thereafter. Conversely, Q approaches Q' when DBH (D) is small. This suggests that the derived allocation functions reflect the growth restrictions that arise in overmature stands for different species and site classes. Our validation of the model also showed the rationality of NPP allocation using analytical functions. The study thus provided a realistic approach to partitioning NPP in modeling the carbon dynamics of Canadian boreal forest ecosystems.

Acknowledgments

We thank Cindy R. Myers and the Oak Ridge National Laboratory's Distributed Active Archive Center (ORNL DAAC) for providing field data from the Boreal Ecosystem-Atmosphere Study (BOREAS), and D. Schultz of the Abitibi-Consolidated Company of Canada for providing field data. This project has been supported by the Natural Sciences and Engineering Research Council of Canada's (NSERC) discovery grants the Canada Research Chair Program, and partly supported by Chinese National Science Foundation (CNSF 40228001).

Appendix A

von Bertalanffy (1957) formulated the growth rate of organisms by following Pütter's (1920) reasoning that growth in weight is the resultant of the difference between anabolic

(building up) and katabolic (breaking down) factors. The growth function (e.g., the increase in the dry weight of biomass) in this process is written as follows:

$$\frac{dw_s}{dt} = pw_s^m - qw_s \tag{A1.1}$$

Solving this differential equation by $\int (pw_s^m - qw_s)dt$, we obtain the Richards function (Richards, 1959):

$$w_s = A(1 - be^{-kt})^{1/(1-m)} \tag{A1.2}$$

where $A = (p/q)^{1/(1-m)}$, $k = p(1 - m)$, and $b = 1 - (w_s|_{t=0}/A)^{(1-m)}$. Let $m=2$ for woody plants. Eq. (A1.2) becomes a logistic growth function, of which the first derivative represents the growth rate:

$$\frac{dw_s}{dt} = -Akbe^{-kt}(1 - be^{-kt})^{-2} \tag{A1.3}$$

Since $be^{-kt} = 1 - A/w_s$ using Eq. (A1.2) and $m=2$, it follows that:

$$\frac{dw_s}{dt} = kw_s(1 - w_sA^{-1}) \tag{A1.4}$$

which can also be derived by expressing p and q with $A[A = (q/p)^{1/(1-m)}$ and $m=2]$ and $k[k = p(1 - m)$ and $m=2]$ in Eq. (A1.1). Then, substituting Eq. (A1.4) for the second item of Eq. (6), it leads to:

$$Q = \left(\frac{dw_f}{dt}\right) \left(\frac{dw_s}{dt}\right)^{-1} + r_f w_f [kw_s(1 - w_sA^{-1})]^{-1} \tag{A1.5}$$

If we accept DBH as a variable that reflects and describes the total biomass of a tree, Eq. (2) can be rewritten as (A1.6) by converting $f_{(w)}$ into $g_{(D)}$, i.e., by expressing w_i using D instead of W :

$$w_i = \alpha_i D^{\beta_i} \quad (i = f, r, s) \tag{A1.6}$$

Substituting Eq. (A1.6) into Eq. (A1.5) gives a function with only one independent variable (D):

$$Q = \left[\frac{d(\alpha_f D^{\beta_f})}{dt}\right] \left[\frac{d(\alpha_s D^{\beta_s})}{dt}\right]^{-1} + r_f \alpha_f D^{\beta_f} [k\alpha_s D^{\beta_s} (1 - \alpha_s D^{\beta_s} A^{-1})]^{-1} \tag{A1.7}$$

Resolving the first item of Eq. (A1.7) gives the following analytical function:

$$Q = (\alpha_f \beta_f) (\alpha_s \beta_s)^{-1} (D^{\beta_f - \beta_s}) + r_f \alpha_f D^{\beta_f} [k\alpha_s D^{\beta_s} (1 - \alpha_s D^{\beta_s} A^{-1})]^{-1} \tag{A1.8}$$

Stem biomass (kg) can be converted from total tree volume (m^3) using the carbon density ($t\text{ C m}^{-3}$) of the wood. We assume:

$$A = 2000h\nu_{\max} \tag{A1.9}$$

where 2000 is a coefficient of unit conversion and h is the carbon density (0.23 t C m^{-3}) estimated by Zhou et al. (2004) for

black spruce. Substituting Eq. (A1.9) into Eq. (A1.8), and rearranging it, we can obtain the final function:

$$Q = (\alpha_f \beta_f) (\alpha_s \beta_s)^{-1} (D^{\beta_f - \beta_s}) + r_f \alpha_f (k\alpha_s)^{-1} (D^{\beta_f - \beta_s}) \times [1 - \alpha_s D^{\beta_s} (2000h\nu_{\max})^{-1}]^{-1} \tag{A1.10}$$

Note that Eq. (A1.10) must meet the restriction that $\alpha_s D^{\beta_s} \leq A$, and Q' is expressed as follows:

$$Q' = (\alpha_f \beta_f) (\alpha_s \beta_s)^{-1} (D^{\beta_f - \beta_s}) \tag{A1.11}$$

Appendix B

Rewriting Eq. (1) provides:

$$\eta_s + \eta_{\text{coarse}} + \eta_{\text{fine}} + \eta_f = 1 \tag{A2.1}$$

$$\eta_s + Q_{\text{croot_stem}} \eta_s + Q_{\text{root_foliage}} \eta_f + \eta_f = 1 \tag{A2.2}$$

$$\eta_s + Q_{\text{croot_stem}} \eta_s + Q_{\text{root_foliage}} Q \eta_s + Q \eta_s = 1 \tag{A2.3}$$

Rearranging Eq. (A2.3) gives the simplified function:

$$\eta_s = [1 + Q_{\text{croot_stem}} + (1 + Q_{\text{root_foliage}})Q]^{-1} \tag{A2.4}$$

REFERENCES

Aldred, A.H., Alemdag, I.S., 1988. Guidelines for forest biomass inventory. Information Report PI-X-77, Petawawa National Forestry Institute.

Battaglia, M., Sands, P.J., Candy, S.G., 1999. Hybrid growth model to predict height and volume growth in young *Eucalyptus globules* plantations. For. Ecol. Manage. 120, 193–201.

Bossel, H., 1996. TREEDYN3 forest simulation model. Ecol. Model. 90, 187–227.

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

CCCMA, 2003. Canadian Centre for Climate Modelling and Analysis. Environment Canada, Meteorological Service of Canada. CGCM2 Data (zip files) [WWW document]. URL <http://www.cccma.bc.ec.gc.ca/cgi-bin/data> (cited 2 July 2003).

Chen, W., Chen, J., Price, D.T., Cihlar, J., 2002. Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada. Can. J. For. Res. 32, 833–842.

Covington, W.W., 1981. Changes in forest floor organic matter and nutrient following clear cutting in northern hardwoods. Ecology 62 (1), 41–48.

Elkie, P.C., Towill, W.D., Ride, K.R., McIlwrath, D.L., 2000. Ontario Land Inventory Primeland/site Information System (OLIPIS). Ont. Min. Natur. Resour. Northwest Sci. Technol. Thunder Bay, Ont. NWST Technical Manual TM-005.

Environment Canada, 1994. Canadian Monthly Climate Data. 1961–1990 Normals on CD-ROM Version 3.0E.

Environment Canada, 2004. Canada's Greenhouse Gas Inventory, 1990–2002. Greenhouse Gas Division, Environment Canada, Ottawa, Canada.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., 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), 29029–29041.

- Hendrick, R.L., Pregitzer, K.S., 1993. Patterns of fine root mortality in two sugar maple forests. *Nature* 361, 59–61.
- Hoffmann, F., 1995. FAGUS, a model for growth and development of beech. *Ecol. Model.* 83, 327–348.
- Kirschbaum, M.U.F., 1999. CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecol. Model.* 118, 17–59.
- Kollomäki, M., 1998. Ecological simulation model for studying diversity of stand structure in boreal forests. *Ecol. Model.* 111, 17–36.
- Landsberg, J.J., Waring, R.H., 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95, 209–228.
- McMurtrie, R.E., Landsberg, J.J., 1992. Using a simulation model to evaluate the effects of water and nutrients on the growth and carbon partitioning of *Pinus radiata*. *For. Ecol. Manage.* 52, 243–261.
- McMurtrie, R.E., Wolf, L., 1983. Above- and below-ground growth of forest stands: a carbon budget model. *Ann. Bot.* 52, 437–448.
- Metherell, A.K., Harding, L.A., Cole, C.V., Parton, W.J., 1993. CENTURY Soil Organic Matter Model Environment Technical Documentation Agroecosystem Version 4.0. GPSR Technical Report No. 4, United States Department of Agriculture, Agricultural Research Service, Great Plains Systems Research Unit. URL <http://www.nrel.colostate.edu/projects/century/> (cited 10 May 2004).
- Mouillot, F., Rambal, S., Lavorel, S., 2001. A generic process-based simulator for Mediterranean landscapes (SIERRA): design and validation exercises. *For. Ecol. Manage.* 147, 75–97.
- Newcomer, J., Landis, D., Conrad, S., Curd, S., Huemrich, K., Knapp, D., Morrell, A., Nickeson, J., Papagno, A., Rinker, D., Strub, R., Twine, T., Hall, F., Sellers, P., 2000. Collected Data of the Boreal Ecosystem-Atmosphere Study. CD-ROM, TE-06. The BOREAS Information System, NASA Goddard Space Flight Center.
- Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.-C., Seastedt, T., Garcia Moya, E., Kamnalrut, A., Kinyamario, J.I., 1993. Observations and modeling biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem. Cyc.* 7, 785–809.
- Pearson, J.A., Fahey, T.J., Knight, D.H., 1984. Biomass and leaf area in contrasting lodgepole pine forests. *Can. J. For. Res.* 14, 259–265.
- Peng, C., Liu, J., Dang, Q., Apps, M.J., Jiang, H., 2002. TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. *Ecol. Model.* 153, 109–130.
- Plonski, W.L., 1974. Normal Yield Tables (metric) for Major Forest Species of Ontario. Division of Forests, Ontario Ministry of Natural Resources, pp. 4–39.
- Pütter, A., 1920. Studien über physiologische Ähnlichkeit. Part VI. Wachstumsähnlichkeiten. *Pfluegers Archiv für die Gesamte Physiologie des Menschen und der Tiere* 180, 298–317.
- Rasse, D.P., Francois, L., Aubinet, M., Kowalski, A.S., Walle, I.V., Laitat, E., Gerard, J., 2001. Modelling short-term CO₂ fluxes and long-term tree growth in temperate forests with ASPECTS. *Ecol. Model.* 141, 35–52.
- Richards, F.J., 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10, 290–300.
- Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional applications. Part I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Model.* 42, 125–154.
- Ryan, M.G., Lavigne, M.B., Gower, S.T., 1997. BOREAS special issue. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Can. J. Geophys. Res.* 102 (D24), 28871–28883.
- Schall, P., 1991. Productivity and vitality of spruce stands: dynamic feedback simulation for responses to different annual and seasonal levels of magnesium supply from soil. *Vegetation* 92, 111–118.
- Sellers, P.J., Hall, F.G., Kelly, R.D., Black, A., Baldocchi, D., Berry, J., Ryan, M., Ranson, K.J., Crill, P.M., Lettenmaier, D.P., Margolis, H., Cihlar, J., Newcomer, J., Fitzjarrald, D., Jarvis, P.G., Gower, S.T., Halliwell, D., Williams, D., Goodison, B., Wickland, D.E., Guertin, F.E., 1997. BOREAS in 1997: experiment overview, scientific results, and future directions. *J. Geophys. Res.* 102 (D24), 28731–28770.
- Siltanen, R.M., Apps, M.J., Zoltai, S.C., Mair, R.M., Strong, W.L., 1997. A Soil Profile and Organic Carbon Data Base for Canadian Forest and Tundra Mineral Soils. Northern Forestry Centre, Canadian Forest Service, pp. 2–50.
- Tiktak, A., Grinsven, H.J.M., 1995. Review of sixteen forest–soil–atmosphere models. *Ecol. Model.* 83, 35–53.
- van Dam, D., van Breemen, N., 1995. NICCCE: a model for cycling of nitrogen and carbon isotopes in coniferous ecosystems. *Ecol. Model.* 79, 255–275.
- von Bertalanffy, L., 1957. Quantitative laws in metabolism and growth. *Quant. Rev. Biol.* 32, 217–231.
- Waring, R.H., 2000. A process model analysis of environmental limitations on the growth of Sitka spruce plantations in Great Britain. *Forestry* 73 (1), 65–79.
- Weinstein, D.A., Beloin, R.M., Yanai, R.D., 1991. Modelling changes in red spruce carbon balance in response to interacting ozone and nutrient stresses. *Tree Physiol.* 9, 127–146.
- Zhou, X., Peng, C., Dang, Q., 2004. Assessing the generality and accuracy of the TRIPLEX model using in situ data of boreal forests in central Canada. *Environ. Model. Softw.* 19, 35–46.