

Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP

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Abstract: In the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS2), root biomass and dynamics are estimated using regression equations based on the literature. A recent analysis showed that some of these equations might overestimate belowground net primary production (NPP_B). The objectives of this study were to update the compilation of root biomass and turnover data, to recalculate the regression equations and to evaluate the impact of the new equations on CBM-CFS2 estimates of net primary production (NPP) and net ecosystem production (NEP). We updated all equations based on 635 pairs of aboveground and belowground data compiled from published studies in the cold temperate and boreal forests. The new parameter for the equation to predict total root biomass for softwood species changed only slightly, but the changes for hardwood species were statistically significant. A new equation form, which improved the accuracy and biological interpretation, was used to predict fine root biomass as a proportion of total root biomass. The annual rate of fine root turnover was currently estimated to be 0.641 of fine root biomass. A comparison of NPP estimates from CBM-CFS2 with results from field measurements, empirical calculations and modeling indicated that the new root equations predicted reasonable NPP_B values. The changes to the root equations had little effect on NEP estimates.

Résumé : Dans le modèle du bilan de carbone du secteur canadien des forêts (CBM-CFS2), la biomasse racinaire et sa dynamique sont estimées à l'aide d'équations de régression basées sur la littérature. Une analyse récente a montré que quelques-unes de ces équations pourraient surestimer la productivité primaire nette souterraine (PPN_S). Cette étude avait pour objectif d'actualiser la compilation des données de biomasse et des données de renouvellement des racines pour recalculer les équations de régression et pour évaluer l'impact des nouvelles équations sur les estimés de productivité primaire nette (PPN) et de productivité nette de l'écosystème (PNE) obtenus avec le modèle CBM-CFS2. Nous avons actualisé toutes les équations sur la base de 635 paires de données sur les composantes aérienne et souterraine recueillies à partir d'études publiées sur les forêts tempérées froides et boréales. Le nouveau paramètre de l'équation utilisée pour prédire la biomasse racinaire totale des espèces résineuses a seulement faiblement changé alors que les changements pour les espèces feuillues étaient statistiquement significatifs. Une nouvelle forme d'équation, qui améliore la précision et l'interprétation biologique, a été utilisée pour prédire la biomasse des racines fines à partir d'une proportion de la biomasse racinaire totale. Le taux annuel de renouvellement des racines fines est actuellement estimé à 0,641 de la biomasse des racines fines. Une comparaison entre des estimés de PPN obtenus avec le CBM-CFS2 et les résultats de mesures sur le terrain, de calculs empiriques et de modélisation montrent que les nouvelles équations racinaires prédisent des valeurs réalistes de PPN_S . Les changements effectués aux équations racinaires ont peu d'effet sur les estimés de PNE.

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Introduction

Modeling is an important approach in the study of carbon cycling in forest ecosystems, but model development has long been hampered by limited quantitative description of the dynamics of belowground biomass. Most existing techniques to measure fine root biomass and production are labor intensive and controversial (Vogt et al. 1998), and this has resulted in a scarcity of accurate estimates on roots relative to the aboveground components. Various methods, both direct and indirect, have been used to measure fine root biomass and production, but no one technique has been accepted universally as the best (Vogt et al. 1998). The

complexity of forest ecosystems per se has also contributed to the slow development of quantitative relationships. Belowground spatial heterogeneity is large (Haynes and Gower 1995; Vogt et al. 1998), and the allocation of photosynthate to fine roots in trees is highly variable (Vogt et al. 1996). Belowground carbon allocation, including fine root growth and senescence, is subject to many biotic and abiotic factors that vary spatially and over time. These factors include stand or tree age, tree species, soil temperature, moisture, and nutrient availability, as well as impacts by insects, fungi, and other soil organisms (Gill and Jackson 2000; Gower et al. 2001; Haynes and Gower 1995; Hendrick and Pregitzer 1993a, 1993b; Nadelhoffer et al. 1985; Pastor and Post 1986; Ryan et al. 1997). Furthermore, when the temporal or spatial scale of interest changes (as may be the case for different modelling approaches), the relative importance of the controlling factors may change accordingly; therefore, findings obtained at one scale may not hold at another (Bloomfield et al. 1996; Gower et al. 1996; Raich and Nadelhoffer 1989).

Because root biomass represents a significant proportion of total ecosystem biomass and root production accounts for a large proportion of the net primary production (NPP) (see Vogt et al. 1991, 1996), robust methods for estimating root biomass and production are important. In the absence of adequate understanding of the relevant ecophysiological processes, empirical approaches are an effective way to use existing, although sparse, data. In the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS2), aboveground biomass dynamics are simulated using biomass accumulation curves derived from the national forest biomass inventory (Bonnor 1985) and a later forest inventory, CanFI 1986 (Forestry Canada 1988). Unfortunately, the national forest inventory does not contain information on roots. As an alternative, several empirical relationships were developed from independent data sets to derive belowground biomass dynamics from aboveground biomass estimates. The belowground components include total root biomass for each species group (i.e., softwood and hardwood), fine root biomass (as a proportion of the total root biomass), and their production (Kurz et al. 1996).

The equations describing root dynamics in the CBM-CFS2 (Kurz and Apps 1999) are based on regression relations derived from published studies in temperate and boreal forest ecosystems covering a wide geographic range (Kurz et al. 1996). Since these relations were originally described (Kurz et al. 1996), a comparison of the CBM-CFS2 estimates of forest NPP with data and other estimates for the Canadian Prairie Provinces has been performed (Li et al. 2002). This analysis indicated that the model may tend to overestimate belowground NPP (NPP_B). For this reason, and acknowledging the widespread interest in forest NPP as an environmental response indicator (Gower et al. 2001; Kimball et al. 2000), it was decided to re-examine the belowground empirical relationships described by Kurz et al. (1996). The objectives of the present study were (i) to review the recent literature and add any new root biomass and production data to the existing database, (ii) to reanalyze the regression relations underlying the root equations used in the CBM-CFS2, and (iii) to evaluate the effect of the update on

CBM-CFS2 estimates of NPP and NEP (net ecosystem production).

Materials and methods

Data from published studies

A database of root studies was previously compiled from the literature (Kurz et al. 1996). This database still serves as the primary data source in the current study but has been substantially updated with data from a broader literature review. The new literature review was aimed particularly at the least certain relationships, such as the estimation of fine root biomass and turnover, where more supporting data are needed to address suspected errors in NPP estimation.

The root diameter used by different investigators to separate coarse and fine roots generally varies from 2 to 5 mm (1 mm was used occasionally) (Vogt et al. 1996). In this study, the distinctions between fine and coarse roots used by the original investigators were maintained. In the present compilation, the same rules used previously (Kurz et al. 1996) were followed: (i) in those few studies where data were provided for more than one diameter limit (e.g., <2 mm and <5 mm), only the estimate with the larger limit was compiled; (ii) in the few studies where more than one method was used for the same measurement, only the method deemed to provide the most reliable estimate was chosen; and (iii) care was taken to avoid duplicate entries of the same data from different sources.

The updated database, in particular the data set for estimating fine root production, includes primarily studies from the cold temperate and boreal forest ecosystems with no further spatial segregation. The available sample size is inadequate to allow further stratification into, for example, the major ecoclimatic zones of Canada. Moreover, the moderate and warm temperate forests account for a very small portion (<10%) of the Canadian forests (Ecoregions Working Group 1989).

The new database contains 635 pairs of data, i.e., data pairs of aboveground–belowground biomass, fine root – total root biomass, and fine root biomass – production (Table 1), which is an increase of about 50% from that used in the previous analysis (Kurz et al. 1996). These data can be grouped into three data sets. The first data set contains 443 pairs of total above- and below-ground biomass (340 and 103 pairs for softwood and hardwood species, respectively). The second includes 90 pairs of total root and fine root biomass data, and the third contains 102 pairs of fine root biomass and fine root production data. These data were compiled from published studies in Canada, northern and central Europe, the former USSR, the United States, Japan, and New Zealand. The main literature sources are presented in Table 2. The database is available at the ftp site <http://carbon.cfs.nrcan.gc.ca/>.

Assumptions and regression analysis

For the purpose of the current analysis we assume that (i) total root biomass (dependent variable) can be estimated from total aboveground biomass (independent variable), (ii) fine root biomass (dependent variable expressed as a proportion of the total root biomass) can be estimated from

Table 1. Regional distribution of the number of sites included in the compiled studies.

Country or region	Total root biomass		Fine root proportion	Fine root production
	Softwood	Hardwood		
Canada	35	3	18	15
Northern Europe ^a	24	15	14	7
Central Europe ^b	21	15	5	9
The former USSR	191	32	18	1
The United States	67	37	35	69
Others ^c	2	1	0	1
Total	340	103	90	102

^aDenmark, Finland, Norway, and Sweden.^bBelgium, Britain, Bulgaria, Czechoslovakia, France, and Germany.^cJapan and New Zealand.

total root biomass (independent variable), and (iii) fine root production (dependent variable) can be estimated from fine root biomass (independent variable). In reality, the factors governing the processes underlying these relationships at the ecosystem level are diverse and complex (Bloomfield et al. 1996; Coomes and Grubb 2000; Hendricks et al. 1993). As demonstrated by Kurz et al. (1996) the relationships are non-linear. The rationale for these three basic assumptions, which provide the conceptual basis for the empirical analyses, was given in Kurz et al. (1996).

Regression analyses of the new data sets were not limited to the equations reported previously by Kurz et al. (1996). Instead, data were fitted to a number of selected equations using SAS (SAS Institute Inc. 1989) for the best fit. Data for the two species groups (hardwood and softwoods) were separately fitted, but the data were combined if the fit led to a nonsignificant equation for either of them. In cases when the intercept was not statistically significant ($P > 0.05$), the equation was forced through the origin.

NPP and NEP estimation with the CBM-CFS2

NPP estimation

The CBM-CFS2 was used in a previous study to simulate changes in carbon pools and fluxes of Canadian forest ecosystems from 1920 to 1989 (Kurz and Apps 1999). At each time step in the simulation, aboveground biomass accumulation was estimated using ecosystem-specific growth curves. The biomass was allocated to various aboveground components using linear regression models derived from the national forest biomass inventory data (Bonnor 1985), and root biomass components were obtained using the equations in Kurz et al. (1996). Annual litterfall was estimated as a proportion of each biomass component and varied with species and location. Any increase in deadfall associated with stand breakup (if indicated in the inventory data, during the over-mature phase, for example) was calculated by comparing the size of the biomass pools at two subsequent time steps. For each of the seven types of disturbances in the model (Kurz et al. 1992; Kurz and Apps 1999), a specific disturbance matrix was used to simulate carbon mass transfers between ecosystem pools, to the atmosphere (e.g., wildfire), and to the forest product sector (e.g., harvesting) at the time of disturbance.

At the end of each time step (5 years in the retrospective simulation 1920–1989), the model outputs a large number of records, each of which represents the state variables for groups of stands having similar ecological characteristics. These state variables include, for each species group, information on area, biomass increment, biomass by component, litterfall, and other detrital inputs, as well as estimates of the carbon in the various dead organic matter pools (Kurz and Apps 1999). For a given time step t , therefore, the forest NPP for the entire region (NPP_{*t*}) can be calculated using the equation:

$$[1] \quad \text{NPP}_t = \sum_{i=1}^n \eta_i (G_{t,i} + L_{t,i})$$

where n is the number of records, η_i is the area fraction associated with record i , and $G_{t,i}$ and $L_{t,i}$ are the biomass increment and detrital input (litterfall and deadfall) of record i , respectively, for that time step (Li et al. 2002). The turnover rate of coarse roots is assumed to be 2% in the CBM-CFS2 (Kurz et al. 1996).

NEP estimation

Dead organic matter (DOM) (i.e., forest floor litter, coarse woody debris, and soil organic matter) in the CBM-CFS2 is accumulated in four pools (designated very fast, fast, medium, and slow) according to its structural origin and decomposability. The first three of these pools may be loosely associated with decomposing forest floor detritus (above- and below-ground), and the slow pool, with soil organic matter. Each of these pools is initially assigned a base decomposition rate (i.e., 0.5, 0.14, 0.037, and 0.0068/year, respectively) at 10°C that is modified according to location by the prevailing mean annual temperature using a $Q_{10} = 2.0$ relationship. In addition, the base decomposition rates of the forest floor detritus (not the slow pool) is adjusted with a factor that varies with the degree of canopy closure to simulate changes in decomposition rates in recently disturbed stands (Kurz et al. 1992; Kurz and Apps 1999). Heterotrophic respiration in any time step t (Rh_t) is estimated as the net carbon release to the atmosphere in that time step from the decomposition of the four DOM pools:

$$[2] \quad Rh_t = \sum_{i=1}^n \eta_i Rh_{t,i}$$

Table 2. Main sources for data collection.

Source	Estimation data		
	Total root biomass	Fine root proportion	Fine root production
(1) Aber et al. 1985			X
(2) Alban et al. 1978	X		
(3) Alexeyev and Birdsey 1994	X		
(4) Arthur and Fahey 1992	X	X	X
(5) Axelsson and Brakenhielm 1980	X	X	
(6) Baskerville 1966	X		
(7) Burke and Raynal 1994			X
(8) Cannell 1982	X	X	
(9) Cole and Rapp 1981	X		
(10) Comeau and Kimmins 1989	X	X	
(11) Coopersmith 1986			X
(12) DeAngelis et al. 1981	X	X	
(13) Finér and Laine 1998			X
(14) Ford and Deans 1977		X	X
(15) Goaster et al. 1991	X	X	
(16) Gower et al. 1997	X		
(17) Grier 1976	X		
(18) Grier and Logan 1977	X	X	
(19) Grier et al. 1981	X	X	X
(20) Haynes and Gower 1995		X	
(21) Helmisaari 1995	X	X	
(22) Helmisaari and Hallbäcken 1999			X
(23) Hendrick and Pregitzer 1993a, 1993b			X
(24) Kajimoto et al. 1999		X	X
(25) Keyes and Grier 1981	X	X	X
(26) Kurz 1989	X	X	X
(27) Lakida et al. 1995	X		
(28) Linder and Axelsson 1982	X	X	
(29) Mälikönen 1975a, 1975b		X	X
(30) Makkonen and Helmisaari 1999			X
(31) McClaugherty et al. 1982			X
(32) Nadelhoffer et al. 1985			X
(33) Persson 1978, 1980a, 1980b			X
(34) Peterson et al. 1983	X	X	
(35) Ruark and Bockheim 1987	X	X	
(36) Ruess et al. 1996		X	X
(37) Santantonio and Hermann 1985			X
(38) Santantonio et al. 1977	X		
(39) Steele et al. 1997		X	X
(40) Turner 1975	X		
(41) Van Praag et al. 1988			X
(42) Viereck et al. 1983	X		
(43) Vogt 1987	X		
(44) Vogt 1991	X	X	X
(45) Vogt et al. 1986	X		X
(46) Vogt et al. 1987	X	X	
(47) Vogt et al. 1990	X		
(48) Vogt et al. 1996	X	X	
(49) Yin et al. 1989		X	X

Thus, the NEP in time step t (NEP_t) can be calculated using

$$[3] \quad NEP_t = NPP_t - Rh_t$$

In the present study, a 1-year time step (rather than the 5-year time step used by Kurz and Apps (1999)) was used. To facilitate comparisons of NPP using the new root relationships with the earlier results using the original relationships (Li et al. 2002), we report only the means (per square

metre of forest area) of NPP and NEP for the period 1991–1995 and restrict the regional analysis to the forests of the Canadian Prairie Provinces (i.e., Alberta, Saskatchewan, and Manitoba).

Results

Empirical relationships supported by the updated database

The data set for total root biomass estimation contains 340 and 103 pairs of aboveground and root biomass data for softwood and hardwood species groups, respectively (Table 1). Separate regression equations were successfully fit to the data for both species groups. For the softwood species group, the data for fine root proportion (75 data pairs) and production (67 data pairs) prediction yielded statistically significant equations, but this was not the case with the data for the hardwood species group. Therefore, data for the two species groups were combined, and four equations were fitted:

$$[4] \quad RB_s = 0.222AB_s$$

$$[5] \quad RB_h = 1.576AB_h^{0.615}$$

$$[6] \quad P_f = 0.072 + 0.354 e^{-0.060RB}$$

$$[7] \quad FRT = 0.641FRB$$

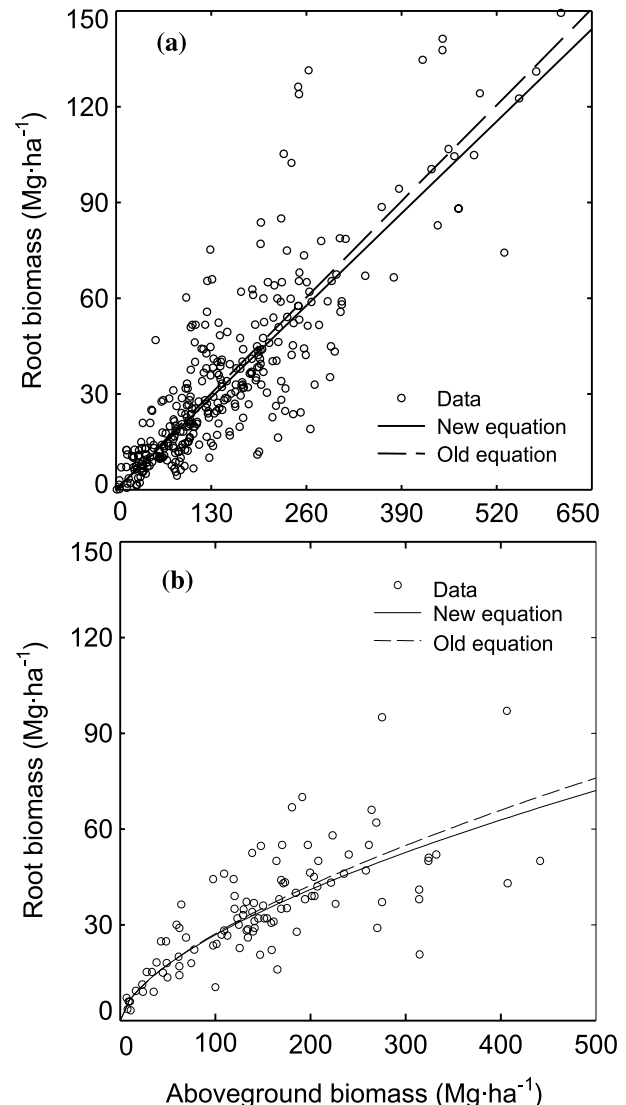
where RB and AB are root and aboveground biomass, respectively; subscripts s and h are softwood and hardwood species groups, respectively; P_f is the fine root proportion of the total root biomass RB; FRT is the fine root turnover; and FRB is the fine root biomass. These relationships are plotted in Figs. 1–3 and summarized in Table 3. With the exception of eq. 5, all functions were forced to pass through the origin because their intercepts were not significant ($P > 0.05$).

Equations for total root biomass prediction for both species groups (eqs. 3 and 4) take exactly the same form as their old counterparts (see Kurz et al. 1996). The numerical differences in the parameter values are small, although the difference between the old and new equations for softwood species is statistically significant ($P < 0.05$), and have only a small influence on the estimates of biomass. In case of softwoods, for example, the current equation predicts a total root biomass that is 4.4% smaller than that predicted with the original parameters. For hardwoods, the old and new parameters yield differences of between 5 and 10% when total AB_h is in the range of 1–7 $Mg \cdot ha^{-1}$ but fall below 5% when AB_h exceeds 7 $Mg \cdot ha^{-1}$.

The new equation for fine root proportion (eq. 6), however, differs from the original in form, and this has an important influence on the magnitude of P_f , especially at low biomass values. In the new relationship, P_f has a maximum value of 0.426, compared with the original equation that was arbitrarily constrained to 0.9. It, therefore, predicts smaller P_f values than the original equation when RB is smaller than about 68 $Mg \cdot ha^{-1}$. For RB values greater than 68 $Mg \cdot ha^{-1}$ the new estimates are somewhat higher than the old (Fig. 2).

No statistical test of the significance of the difference in the equation for fine root proportion (eq. 6) was applied, as we were unable to find a suitable test that compares the change in both data and equation form. However, the new equation is based on a much larger sample size ($n = 91$ instead of 16), has a higher r^2 ($r^2 = 0.362$ rather than 0.278), is statistically more significant ($P < 0.001$ instead of $P =$

Fig. 1. Relationships between total root biomass and above-ground biomass for (a) the softwood species group (difference between the old and new equations is significant at $P < 0.05$) and (b) the hardwood species group (difference between the old and new equations is not significant at $P < 0.05$). The old equation is the original equation in Kurz et al. (1996), and the new equation is the equation from this study.



0.036), and is biologically more reasonable at low biomass values than the original. The lower biomass is largely responsible for belowground NPP estimates that are in much better agreement with observed values as noted by Li et al. (2002).

A linear relationship between fine root turnover and fine root biomass was still found to hold with the new data, but with a turnover rate of 0.641, which is 12.8% smaller than and significantly different from the original estimate of 0.731 (eq. 7). The four new equations are supported at a statistical level of $P < 0.001$ (Table 3).

New equations in estimating forest NPP and NEP

Estimates of forest NPP and NEP for the Canadian Prairie Provinces using the CBM-CFS2 are presented in Table 4 for

Fig. 2. Relationships between the proportion of fine root biomass and total root biomass (equations have different forms). The old equation is the original equation in Kurz et al. (1996), and the new equation is the equation from this study. SW, softwood; HW, hardwood.

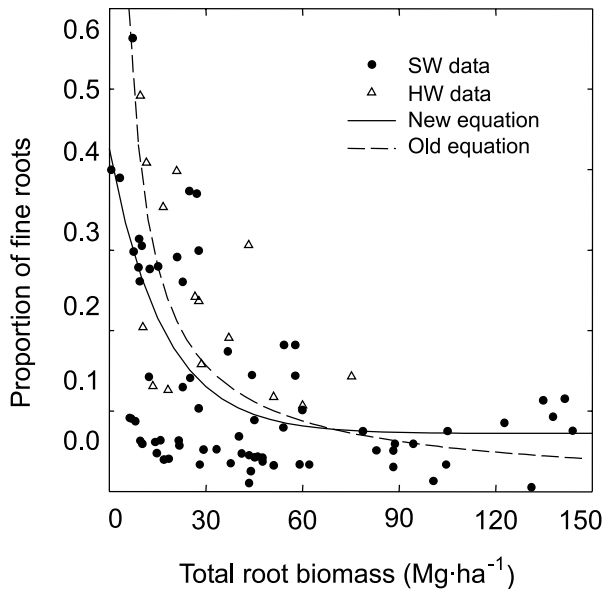
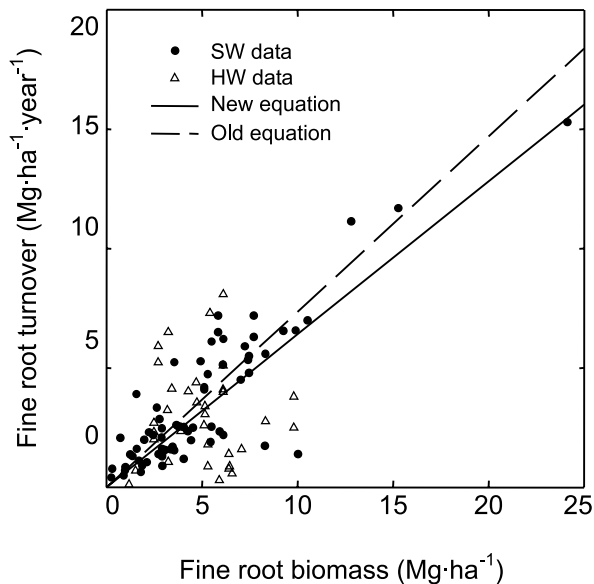


Fig. 3. Fine root production as a function of fine root biomass (difference between equation with the old and new parameters is significant at $P < 0.05$). The old equation uses the original parameters in Kurz et al. (1996), and the new equation uses the parameters from this study. SW, softwood; HW, hardwood.



the period 1991–1995. The new equations for root biomass and dynamics, as expected, had no influence on the estimation of aboveground NPP (NPP_A). They yielded substantially smaller values for NPP_B than the old equations, however. The reduction in NPP_B estimates was primarily due to the large reduction in estimates of fine root production (NPP_{fr}), offset by a small increase in the estimates of coarse root production (NPP_{cr}). Thus, for instance, with the new relation-

ships, NPP_B of the subarctic, boreal, grassland, and cordilleran eco-provinces was estimated to be 35.5% smaller, on average, than the original estimates. This decrease includes a mean decrease of 39.4% for NPP_{fr} and a slight increase in NPP_{cr} (Table 4).

With the new root relationships, total NPP (NPP_T , including above- and below-ground) of the subarctic, boreal, grassland, and cordilleran forests was 152, 300, 293, and 394 $g\ C\cdot m^{-2}\cdot year^{-1}$, respectively. The contribution of belowground production to the total (NPP_B/NPP_T) ranged from 0.43–0.55 with a mean of 0.47. With the original equations, the model yielded estimates of NPP_T that are about 25.7% higher; for the same forests the original belowground proportions (NPP_B/NPP_T) varied from 0.51 to 0.70 with a mean of 0.59.

The new equations were also found to substantially lower the estimates for Rh. For example, the new estimates of DOM pool decomposition for the Prairie Province forest ecosystems were 165–341 $g\ C\cdot m^{-2}\cdot year^{-1}$, depending on the ecoclimatic provinces. These values are 14.0–29.5% smaller than the values predicted with the original equations. Because NEP is calculated as NPP minus Rh, and the new estimates of NPP and Rh are reduced by similar amounts, the NEP estimates were not greatly affected by the new root equations (Table 4). The mean NEP for the region changed from 33 $g\ C\cdot m^{-2}\cdot year^{-1}$ with the old equations to 26 $g\ C\cdot m^{-2}\cdot year^{-1}$ with the new ones.

Discussion

Empirical relationships: tools for extending aboveground information

Traditional forest inventories offer a great amount of valuable information on aboveground biomass components. To quantify changes in ecosystem carbon stocks, information on belowground biomass components is also required. Empirical relationships, such as those presented here offer a methodology for extending the inventory information to other ecosystem carbon pools.

Roots of trees can be separated by size, function, and morphology into coarse supportive roots, small-diameter woody roots, and very fine roots ($<2\ mm$) (Bloomfield et al. 1996). In most studies dealing with root biomass and turnover, roots are generally partitioned into ephemeral fine roots and structural coarse roots, with fine roots being defined as roots $\leq 1\text{--}5\ mm$ in diameter (Kurz 1989; Mälikönen 1975a, 1975b; Ruark and Bockheim 1987; Steele et al. 1997). Coarse root biomass is believed to be allometrically correlated with total aboveground biomass (Marklund 1988; Santantonio 1990; Steele et al. 1997), while fine roots typically contribute only a small fraction of the total root biomass (Vogt 1991; Kurz 1989; Keyes and Grier 1981). Conceptually, therefore, it is rational to approximate total root biomass as a function of total aboveground biomass. With data from published studies in different climatic zones, Cairns et al. (1997) found that aboveground biomass by itself accounted for 83% of the variation in root biomass. Cairns et al. (1997), however, reported no differences between tree types. In contrast, our analysis suggests separate equations for softwood and hardwood species (Fig. 1).

Table 3. Variables, estimated parameters, and other statistics for the four regression equations.

Equation No.	Dependent variable	Independent variable	<i>n</i>	Parameter estimate			<i>r</i> ²	<i>P</i>
				<i>a</i>	<i>b</i>	<i>c</i>		
4	SW root biomass	SW aboveground biomass	340 (260)	0.222±0.004			0.799	<0.001
5	HW root biomass	HW aboveground biomass	103 (85)	1.576±0.267	0.615±0.035		0.562	<0.001
6	Fine root proportion	Root biomass	90 (16)	0.072±0.023	0.354±0.063	16.608±5.500	0.362	<0.001
7	Fine root turnover	Fine root biomass	102 (75)	0.641±0.031			0.503	<0.001

Note: Estimates are given ±1 SE. Values of *n* given in parentheses are the numbers of data used in the previous analysis (see Kurz et al. 1996). SW, softwood; HW, hardwood.

Table 4. Net primary production (NPP), heterotrophic respiration (Rh), and net ecosystem production (NEP) estimates of forests in the Canadian Prairie Provinces (Alberta, Saskatchewan, and Manitoba) predicted with the CBM-CFS2.

Ecoclimatic province	Estimate (g C·m ⁻² ·year ⁻¹)						
	NPP _{fr}	NPP _{cr}	NPP _B	NPP _A	NPP _T	Rh	NEP
With root equations from Kurz et al. 1996							
Subarctic forest	158	2	160	68	228	234	-6
Boreal forest	198	15	214	162	376	342	34
Grassland forest	155	17	173	167	339	308	31
Cordilleran forest	253	25	279	204	482	421	62
Entire region	199	15	214	158	372	339	33
With root equations from this study							
Subarctic forest	78	5	84	68	152	165	-14
Boreal forest	120	18	138	162	300	274	27
Grassland forest	106	19	126	167	293	265	27
Cordilleran forest	163	28	191	204	394	341	53
Entire region	120	18	138	158	296	270	26

Note: Values are means from 1991–1995. NPP_{fr}, fine root NPP; NPP_{cr}, coarse root NPP; NPP_B, belowground NPP; NPP_A, aboveground NPP; NPP_T, total NPP.

There are studies in which fine root biomass has been linked with foliage biomass (Cannell and Dewar 1994; Nikinmaa 1992; Vanninen and Mäkelä 1999; Santantonio 1989), and this approach may be a good strategy when foliage data are readily available. In the present case, we estimate the correlation between fine root biomass and total root biomass (eq. 6 and Fig. 2). A similar pattern between fine root and total root biomass was observed by Cairns et al. (1997).

Biases and uncertainties inevitably arise in the estimation of the proportion and turnover of fine roots because of the empirical failure to partition roots with a consistent diameter limit, and the difficulties of distinguishing between softwood and hardwood species. Of the 160 studies reporting fine root biomass in the database, very few reported data for multiple diameter limits. Half (50%) of them did so with a 5-mm diameter limit, with most of the remainder having 3 (19%) or 2 mm (25%). The arbitrary selection of only the largest limit for those few studies providing multiple estimates does not introduce any significant bias. On the other hand, recent evidence suggests a different belowground carbon allocation by the two species groups (Gower et al. 2001, 1999; Vogt et al. 1986); while our data are unable to distinguish this difference in the proportion of fine root biomass (Fig. 2) and fine root turnover (Fig. 3), the total root biomass (Fig. 1) does support this finding.

The importance of fine roots in nutrient uptake and carbon cycling has been widely acknowledged (Bloomfield et al.

1996; Coomes and Grubb 2000; Hendricks et al. 1993), but estimating fine root turnover and production still remains a challenge. Fine roots do not appear to have regular cycles of senescence and are ephemeral (Bloomfield et al. 1996). Large intra- and inter-annual variations in fine root biomass have been reported (Persson 1978, 1980a, 1980b; Santantonio and Hermann 1985; Makkonen and Helmisaari 1999). Warmer soil temperature is believed to be associated with faster turnover of fine roots (Gill and Jackson 2000; Hendrick and Pregitzer 1993a, 1993b). Soil moisture and fertility (e.g., nutrients) are also thought to be important factors influencing belowground carbon allocation and fine root turnover (Nadelhoffer et al. 1985; Pastor and Post 1986; Haynes and Gower 1995). There are studies that suggest that the longevity of fine roots of deciduous tree species is shorter than that of evergreen species and that roots of different size differ in turnover rates (see Bloomfield et al. 1996; Gill and Jackson 2000). As a whole, however, our theoretical understanding of the rate and controls of fine root turnover as well as their relations to tree growth is limited by the paucity of experimental data. Taking an empirical approach, the assumption that fine root production can be estimated from fine root biomass is well supported by the present compiled data (Table 3). The shortcoming of the empirical approach is that it fails to explicitly resolve key eco-physiological processes and may not be robust under changing conditions.

As more studies are performed in cold temperate and boreal forests, improvements to the current root equations may be expected, and with these, increased confidence in the model simulations of belowground NPP and NEP. The present equations, drawn from studies performed over a wide geographic range, are expected to produce valid estimates at regional scales when applied to stands over a range of ecological conditions but may produce significant prediction errors when used for individual stands (Kurz et al. 1996).

One approach for improving the representation of root biomass dynamics at the local or regional scale is through incorporation of adjustment factors to account for such site-specific influences as soil temperature, moisture, fertility (or nutrients), and species (in estimating fine root proportion and turnover). In principle, such adjustment factors would allow the CBM-CFS2 to further differentiate root dynamics for different locations, although in practice, insufficient data are available to calculate such factors.

Implications of the current root equations in estimating NPP and NEP

The CBM-CFS2 is an inventory-based carbon accounting model. It calculates net changes in biomass and DOM stocks to directly estimate NEP and NBP and does not depend on an intermediate calculation of NPP. To facilitate comparisons with process models, however, NPP has recently been added as an output indicator in the model. A previous comparison of the CBM-CFS2 estimates of NPP with the NPP results from various independent approaches showed that the model likely overestimated NPP_B with its original root equations (Li et al. 2002). Here, we conducted a similar comparison using the new equations. The study region (Prairie Provinces of Canada) was selected to make use of the large number of study results from the Boreal Ecosystem–Atmosphere Study (BOREAS) conducted in this region during the 1990s. Most of the NPP and NEP estimates by BOREAS investigators were for the early 1990s, so the CBM-CFS2 analyses were conducted of the same period (1991–1995) to facilitate comparisons. The present results may also be compared against the previous analysis for the same forests (but for the period 1980–1989) using the original root parameters (Kurz et al. 1996) and with ad hoc adjustments to them (Li et al. 2002).

Simulated values of NPP_A with CBM-CFS2 for the boreal forests in Alberta, Saskatchewan, and Manitoba were 138–176 g C·m⁻²·year⁻¹ for the period 1990–1995. This estimate is larger than the field measurements (98–144 g C·m⁻²·year⁻¹) by Gower et al. (1997) for mature black spruce and jack pine stands at the northern (NSA) and southern (SSA) study areas of the BOREAS region but much smaller than their measurements for mature aspen stands (249–316 g C·m⁻²·year⁻¹) (Table 5). Given the dominant presence of softwood (e.g., black spruce and jack pine) over hardwood species (e.g., aspen) in the region (Ecoregions Working Group 1989), the area-weighted NPP_A estimates of the CBM-CFS2 match Gower et al.'s site-specific field results. The model's predicted NPP_A values also are in much closer agreement with the various empirical calculations reviewed by Li et al. (2002) and shown in Table 5.

With the root equations from the current study, the CBM-CFS2 estimated NPP_B values for the boreal forests in Al-

Table 5. Summary of NPP results for forests in Canadian Prairie Provinces using different approaches.

Methodology	Region ^a	Forest type	Period	NPP_A	NPP_B	NPP_T	NPP_B/NPP_T	Reference
Field measurement ^b	NSA, SSA	Aspen	1993–1994	249–316, 288–299	65, 40	303, 313	0.13–0.21	Gower et al. 1997
		Black spruce		111–124, 144–141	90, 120	206, 253	0.43–0.47	Steele et al. 1997
		Jack pine		98–106, 111–112	100, 105	206, 221	0.48	Steele et al. 1997
Empirical calculation ^c	Alberta	Boreal forest	Around 1980	146–154	136–145	283–291	0.48–0.50	Li et al. 2002
	Saskatchewan ^d			123–136	131–140	257–262	0.51–0.53	Li et al. 2002
	Manitoba			138–148	134–143	274–281	0.49–0.51	Li et al. 2002
Modeling	SSA	Boreal forest	1994–1996			170–216		Kimball et al. 2000
	NSA, SSA	Boreal forest	— ^e			254, 268		Peng and Apps 1998
	NSA, SSA	Boreal forest	1994			253, 308		Liu et al. 1999
CBM-CFS2	BOREAS	All forests	1994			316 ^f		Goetz et al. 1999
	Alberta	Boreal forest	1991–1995	171	154	325	0.47	This study
	Saskatchewan			176	127	303	0.42	This study
	Manitoba			138	131	268	0.49	This study

^aNSA and SSA refer to the northern and southern study areas of the Boreal Ecosystem–Atmosphere Study (BOREAS) region, respectively. NSA was located in the northern boreal zone of Manitoba, and SSA in the southern boreal zone of Saskatchewan.

^bRange of NPP_A (not including understory and bryophytes) shows variation between 1993 and 1994, while NPP_B and NPP_T are results for 1994 only. NPP_A , NPP_B , and NPP_T are defined in Table 4.

^cRange of data shows variation between different empirical approaches summarized by Li et al. (2002).

^dCalculated in the same way as was done for Alberta and Manitoba by Li et al. (2002).

^eMeans of the last 100 years of a 5000-year CENTURY simulation with a mean fire return interval of 100 years.

^fMean after excluding land-cover classes defined as agriculture and pasture, recently burned, grasses and marsh, and unknown.

berta, Saskatchewan, and Manitoba to be 154, 127, and 131 g C·m⁻²·year⁻¹, respectively. These estimates are much lower than the values obtained with the old equations (Table 4) and are relatively consistent with calculations from the different empirical approaches. They also are comparable with Steele et al. (1997) field measurements for mature black spruce and jack pine stands but are much larger than their field data for mature aspen stands (Table 5). In general, the current CBM-CFS2 estimates for NPP_B are comparable with the field results of Steele et al. (1997). The proportion of NPP_{cr} in the total NPP_B predicted with our model for the boreal forest (13%) (Table 4) appears much smaller than Steele et al. (1997) estimates (26–31%, except for aspen stand at NSA), and the reason is not clear.

Most models do not distinguish NPP_A and NPP_B. Estimates for NPP_T of forests in the BOREAS region, obtained from other models ranged from 170 to 316 g C·m⁻²·year⁻¹, with a mean of 265 g C·m⁻²·year⁻¹. This is close to our area-weighted mean (285 g C·m⁻²·year⁻¹) for the boreal forests in Saskatchewan and Manitoba where the BOREAS study region is located (Table 5).

The new root equations lower the estimates of fine root biomass and production and, therefore, also the rates of respiration from the decay of dead fine roots. Since both NPP and Rh are reduced, the changes in the equations affect NEP estimates much less than NPP estimates (Table 4). The CBM-CFS2 currently estimates the mean NEP of the boreal forest in the Canadian Prairie Provinces to be 26 g C·m⁻²·year⁻¹ (a sink) for 1991–1995 (Table 4).

Year-round tower measurements indicated that carbon fluxes (NEE or NEP) at the BOREAS tower sites varied from 130 g C·m⁻²·year⁻¹ (a sink) at the SSA old aspen site (Black et al. 1996; Grant et al. 1999) to 50 g C·m⁻²·year⁻¹ at the NSA old black spruce site (Goulden et al. 1997). Over a period of 119 days during active growth, a young jack pine stand at the NSA was measured to be a sink of 200–267 g C·m⁻² (Joiner et al. 1999; McCaughey et al. 1997), while in a similar period in 1994, a sink of 95 g C·m⁻² was measured in an old black spruce stand at the SSA (Jarvis et al. 1997). During the winter, soil respiration at the NSA was estimated to release 40–55 g C·m⁻² to the atmosphere (Winston and Sundquist 1997). The current tower locations are in productive stands (Halliwell and Apps 1997), and the extent to which the tower measurements represent the total area of the boreal forests is unclear. Tower measurements are specific to a particular site, including all vegetation and soil layers at that site, while the CBM-CFS2 accounts for C stock changes in trees (ignoring shrubs, herbs, and mosses) and soil layers over a landscape containing many individual stands. Thus, CBM-CFS2 estimates reported here are multiyear regional means of stands in all age-classes and all stages of stand development. These estimates represent a different population than the stand-specific tower measurements over a single growing season.

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References

- Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A., and Pastor, J. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia*, **66**: 317–321.
- Alban, D.H., Perala, D.A., and Schlaegel, B.E. 1978. Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. *Can. J. For. Res.* **8**: 290–299.
- Alexeyev, V.A., and Birdsey, R.A. 1994. Carbon in ecosystems of forests and peatlands of Russia. Sukachev Institute for Forest Research, Krasnoyarsk, Russia.
- Arthur, M.A., and Fahey, T.J. 1992. Biomass and nutrients in an Engelmann spruce – subalpine fir forest in north-central Colorado: pools, annual production, and internal cycling. *Can. J. For. Res.* **22**: 315–325.
- Axelsson, B., and Brakenhielm, S. 1980. Investigation sites of the Swedish coniferous forest project — biological and physiographical features. In *Structure and function of northern coniferous forests — an ecosystem study*. Edited by T. Persson. *Ecol. Bull.* **32**: 25–64.
- Baskerville, G.L. 1966. Dry-matter production in immature balsam fir stands: roots, lesser vegetation, and total stand. *For. Sci.* **12**: 49–53.
- Black, T.A., den Hartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nesic, Z., Lee, X., Chen, S.G., and Staebler, R. 1996. Annual cycles of water vapor and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biol.* **2**: 219–229.
- Bloomfield, J., Vogt, K., and Wargo, P.M. 1996. Tree root turnover and senescence. In *Plant roots: the hidden half*. Edited by Y. Waisel, A. Eshel, and U. Kafkafi. Marcel Dekker, New York. pp. 363–381.
- Bonnor, G.M. 1985. Inventory of forest biomass in Canada. Canadian Forest Service, Petawawa National Forest Institute, Chalk River, Ont.
- Burke, M.K., and Raynal, D.J. 1994. Fine root growth phenology, production, and turnover in a northern hardwood ecosystem. *Plant Soil*, **162**: 135–146.
- Cairns, M.A., Brown, S., Helmer, E.H., and Baumgardner, G.A. 1997. Root biomass allocation in the world's upland forests. *Oecologia*, **111**: 1–11.
- Cannell, M.G.R. 1982. World forest biomass and primary production data. Academic Press, London.
- Cannell, M.G.R., and Dewar, R.C. 1994. Carbon allocation in trees: a review of concepts for modelling. *Adv. Ecol. Res.* **25**. pp. 59–104.
- Cole, D.W., and Rapp, M. 1981. Elemental cycling in forests. In *Dynamic properties of forest ecosystems*. Edited by D.E. Reichle. Cambridge University Press, London. pp. 341–409.
- Comeau, P.G., and Kimmins, J.P. 1989. Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. *Can. J. For. Res.* **19**: 447–454.
- Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Monogr.* **70**: 171–207.
- Coopersmith, D.J. 1986. Root and fungal biomass production on low, medium and high productivity second-growth Douglas-fir

- stands on Vancouver Island. M.Sc. thesis, Faculty of Forestry, University of British Columbia, Vancouver, B.C.
- DeAngelis, D.L., Gardner, R.H., and Shugart, H.H. 1981. Productivity of forest ecosystems studied during the IBP: the woodlands data set. In *Dynamic properties of forest ecosystems. Edited by D.E. Reichle*. Cambridge University Press, London. pp. 567–672.
- Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Ecoregions Working Group of Canada Committee on Ecological Land Classification, Sustainable Development Branch, Conservation and Protection, Canadian Wildlife Service, Environment Canada, Ottawa, Ont. Ecol. Land Classif. Ser. 23.
- Finér, L., and Laine, J. 1998. Root dynamics at drained peatland sites of different fertility in southern Finland. *Plant Soil*, **201**: 27–36.
- Ford, E.D., and Deans, J.S. 1977. Growth of Sitka spruce plantation: spatial distribution of length, weight and carbohydrate concentrations of fine roots. *Plant Soil*, **47**: 463–485.
- Forestry Canada. 1988. Canada's forest inventory 1986. Forestry Canada, Ottawa, Ont.
- Gill, R.A., and Jackson, R. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytol.* **147**: 13–31.
- Goulden, M.L., Daube, B.C., Fan, S.M., Sutton, D.J., Bazzaz, A., Munger, J.W., and Wofsy, S.C. 1997. Physiological responses of a black spruce forest to weather. *J. Geophys. Res.* **102**(D24): 28 987 – 28 996.
- Gower, S.T., Pongracic, S., and Landsberg, J.J. 1996. A global trend in belowground carbon allocation: can we use the relationship at smaller scales? *Ecology*, **77**: 1750–1755.
- 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.* **104** (D22): 29 029 – 29 041.
- Gower, S.T., Kucharik, C.J., and Norman, J. 1999. Direct and indirect estimation of leaf area index, f_{APAR} , and net primary production of terrestrial ecosystems. *Remote Sens. Environ.* **70**: 29–51.
- Gower, S.T., Krankina, O., Olson, R.J., Apps, M.J., Linder, S., and Wang, C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol. Appl.* **11**: 1395–1411.
- Grant, R.F., Black, T.A., den Hartog, G., Berry, J.A., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., and Nalder, I.A. 1999. Diurnal and annual exchanges of mass and energy between an aspen–hazelnut forest and the atmosphere: testing the mathematical model ECOSYS with data from the BOREAS experiment. *J. Geophys. Res.* **104**(D22): 27 699 – 27 717.
- Grier, C.C. 1976. Biomass production and nitrogen–phosphorus cycles in hemlock–spruce stands of the central Oregon coast. In *Western hemlock management. Edited by W.A. Atkinson and R.J. Zasoski*. University of Washington Press, Seattle, Wash. pp. 71–81.
- Grier, C.C., and Logan, R.S. 1977. Old growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* **47**: 373–400.
- Grier, C.C., Vogt, K.A., Keyes, M.R., and Edmonds, R.L. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can. J. For. Res.* **11**: 155–167.
- Halliwell, D., and Apps, M.J. 1997. BOREAS biometry and auxiliary sites: overstory and understory data. *Can. For. Serv. North. For. Cent. Inf. Rep. F042-266/2-1997E*.
- Haynes, B.E., and Gower, S.T. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiol.* **15**: 317–325.
- Helmisaari, H.S. 1995. Nutrient cycling in *Pinus sylvestris* stands in eastern Finland. *Plant Soil*, **168–169**: 327–336.
- Helmisaari, H.S., and Hallbäck, L. 1999. Fine-root biomass and necromass in limed and fertilized Norway spruce (*Picea abies* (L.) Karst.) stands. *For. Ecol. Manage.* **119**: 99–110.
- Hendrick, R.L., and Pregitzer, K.S. 1993a. Patterns of fine root mortality in two sugar maple forests. *Nature (London)*, **361**: 59–61.
- Hendrick, R.L., and Pregitzer, K.S. 1993b. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Can. J. For. Res.* **23**: 2507–2520.
- Hendricks, J.J., Nadelhoffer, K.J., and Aber, J.D. 1993. Assessing the role of fine roots in carbon and nutrient cycling. *Trends Ecol. Evol.* **8**: 174–178.
- Jarvis, P.G., Massheder, J.M., Hale, S.E., Moncrieff, J.B., Rayment, M., and Scott, S.L. 1997. Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest. *J. Geophys. Res.* **102**(D24): 28 953 – 28 966.
- Joiner, D.W., McCaughey, J.H., Lafleur, P.M., and Bartlett, P.A. 1999. Water and carbon dioxide exchange at a boreal young jack pine forest in the BOREAS northern study area. *J. Geophys. Res.* **104**(D22): 27 641 – 27 652.
- Kajimoto, T., Matsuura, Y., Sofronov, M.A., Volokitina, A.V., Mori, S., Osawa, A., and Abaimov, A.P. 1999. Above- and belowground biomass and net primary productivity of a *Larix gmelinii* stand near Tura, central Siberia. *Tree Physiol.* **19**: 815–822.
- Keyes, M.R., and Grier, C.C. 1981. Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Can. J. For. Res.* **11**: 599–605.
- Kimball, J.S., Keyser, A.R., Running, S.W., and Saatchi, S.S. 2000. Regional assessment of boreal forest productivity using an ecological process model and remote sensing parameter maps. *Tree Physiol.* **20**: 761–775.
- Kurz, W.A. 1989. Net primary production, production allocation, and foliage efficiency in second growth Douglas-fir stands with differing site quality. Ph.D. thesis, University of British Columbia, Vancouver, B.C.
- 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. For. Can. 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.
- Lakida, P., Nilsson, S., and Shvidenko, A. 1995. Estimation of forest phytomass for selected countries of the former European USSR. International Institute for Applied Systems Analysis. Laxenburg, Austria. IIASA Working Pap. WP-95-79.
- Le Goaster, S., Dambrine, E., and Ranger, J. 1991. Croissance et nutrition minérale d'un peuplement d'épicéa sur sol pauvre. I. Évolution de la biomasse et dynamique d'incorporation d'éléments minéraux. *Acta Oecol.* **12**: 771–789.
- Li, Z., Apps, M.J., Banfield, E., and Kurz, W.A. 2002. Estimating net primary production of forests in the Canadian prairie provinces using an inventory-based carbon budget model. *Can. J. For. Res.* **32**: 161–169.
- Linder, S., and Axelsson, B. 1982. Changes in carbon uptake and allocation patterns as a result of irrigation and fertilization in a young *Pinus sylvestris* stand. In *Carbon Uptake and Allocation: Key to Management of Subalpine Forest Ecosystems. Proceedings of an IUFRO Workshop. Edited by R.H. Waring*. Forest Resources Laboratory, Oregon State University, Corvallis, Ore. pp. 38–44.

- Makkonen, K., and Helmisaari, H.S. 1999. Assessing fine-root biomass and production in a Scots pine stand — comparison of soil core and root ingrowth core methods. *Plant Soil*, **210**: 43–50.
- Mälikönen, E. 1975a. Annual primary production and nutrient cycle in some Scots pine stands. *Commun. Inst. For. Fenn.* 84. pp. 1–87.
- Mälikönen, E. 1975b. Annual primary production and nutrient cycle in a birch stand. *Commun. Inst. For. Fenn.* 91. pp. 1–35.
- Marklund, L.G. 1988. Biomass functions for pine, spruce and birch in Sweden. Sveriges Lantbruksuniversitet, Uppsala, Sweden. Inst. Skogstaxering. Rapp. 45.
- McCaughey, J.H., Lafleur, P.M., Joiner, D.W., Bartlett, P.A., Costello, A.M., Jelinski, D.E., and Ryan, M.G. 1997. Magnitudes and seasonal patterns of energy, water, and carbon exchanges at a boreal young jack pine forest in the BOREAS northern study area. *J. Geophys. Res.* **102**(D24): 28 997 – 29 007.
- McClagherty, C.A., Aber, J.D., and Melillo, J.M. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology*, **63**: 1481–1490.
- Nadelhoffer, K.J., Aber, J.D., and Melillo, J.M. 1985. Fine roots, net primary production and soil nitrogen availability: a new hypothesis. *Ecology*, **66**: 1377–1390.
- Nikinmaa, E. 1992. Analyses of the growth of Scots pine: matching structure with function. *Acta For. Fenn.* 235. pp. 1–68.
- Pastor, J., and Post, W.M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry*, **2**: 3–27.
- Persson, H. 1978. Root dynamics in a young Scots pine stand in central Sweden. *Oikos*, **30**: 508–509.
- Persson, H. 1980a. Spatial distribution of fine root growth, mortality and decomposition in a young Scots pine stand in central Sweden. *Oikos*, **34**: 77–87.
- Persson, H. 1980b. Death and replacement of fine roots in a mature Scots pine stand. In *Structure and function of northern coniferous forests — an ecosystem study*. Edited by T. Persson. *Ecol. Bull.* **32**: 251–260.
- Peterson, E.B., Peterson, N.M., and Kabzems, R.D. 1983. Impact of climatic variation on biomass accumulation in the boreal forest zone: selected references. *Environ. Can. For. Serv. North. For. Res. Cent. Inf. Rep.* NOR-X-254.
- Raich, J.W., and Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology*, **70**: 1346–1354.
- Ruark, G.A., and Bockheim, J.G. 1987. Belowground biomass of 10-, 20-, and 32-year-old *Populus tremuloides* in Wisconsin. *Pedobiologia*, **30**: 207–217.
- Ruess, R.W., Cleve, K.V., 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. 214–262.
- Santantonio, D. 1989. Dry-matter partitioning and fine root production in forests — new approaches to a different problem. In *Biomass production by fast-growing trees*. Edited by J.S. Pereira and J.J. Landsberg. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 57–72.
- Santantonio, D. 1990. Modeling growth and production of tree roots. In *Process modeling of forest growth responses to environmental stress*. Edited by R.K. Dixon, R.S. Meldahl, G.A. Ruark, and W.G. Warren. Timber Press, Portland, Oreg. pp. 124–141.
- Santantonio, D., and Hermann, R.K. 1985. Standing crop, production and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. *Ann. Sci. For.* **42**: 113–142.
- Santantonio, D., Hermann, R.K., and Overton, W.S. 1977. Root biomass studies in forest ecosystems. *Pedobiologia*, **17**: 1–31.
- SAS Institute Inc. 1989. SAS/STAT user's guide, version 6. 4th ed. Vol. 1. SAS Institute Inc., Cary, N.C.
- 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.
- Turner, J. 1975. Nutrient cycling in a Douglas-fir ecosystem with respect to age and nutrient status. Ph.D. dissertation, University of Washington, Seattle, Wash.
- Vanninen, P., and Mäkelä, A. 1999. Fine root biomass of Scots pine stands differing in age and soil fertility in southern Finland. *Tree Physiol.* **19**: 823–830.
- Van Praag, H.J., Sougniez-Remy, S., Weissen, F., and Carletti, G. 1988. Root turnover in a beech and a spruce stand of the Belgian Ardennes. *Plant Soil*, **105**: 87–103.
- Viereck, L.A., Dyrness, C.T., Van Cleve, K., and Foote, M.J. 1983. Vegetation, soil, and forest productivity in selected forest types in interior Alaska. *Can. J. For. Res.* **13**: 703–720.
- Vogt, D.J. 1987. Douglas-fir ecosystems in western Washington: biomass and production as related to site quality and stand age. Ph.D. dissertation, University of Washington, Seattle, Wash.
- Vogt, K. 1991. Carbon budgets of temperate forest ecosystems. *Tree Physiol.* **9**: 69–86.
- Vogt, K.A., Grier, C.C., and Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Adv. Ecol. Res.* 15. pp. 303–377.
- Vogt, K.A., Dahlgren, R., Ugolini, F., Zabowski, D., Moore, E.E., and Zasoski, R. 1987. Al, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above- and belowground biomass. II. Pools and circulation in a subalpine *Abies amabilis* stand. *Biogeochemistry*, **4**: 295–311.
- Vogt, K.A., Vogt, D.J., Gower, S.T., and Grier, C.C. 1990. Carbon and nitrogen interactions for forest ecosystems. In *Above- and below-ground interactions in forest trees in acidified soils*. Edited by H. Persson. Commission of the European Communities. Directorate-General for Science, Research and Development, Environment Research Programme, Brussels, Belgium. *Air Pollut. Rep.* 32. pp. 203–235.
- Vogt, K.A., Vogt, D.J., and Bloomfield, J. 1991. Input of organic matter to the soil by tree roots. In *Plant roots and their environment*. Edited by B.L. McMichael and H. Persson. Elsevier Science Publishers, New York. pp. 171–190.
- Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., Hara, J.O., and Asbjornsen, H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil*, **187**: 159–219.
- Vogt, K.A., Vogt, D.J., and Bloomfield, J. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant Soil*, **200**: 71–89.
- Winston, G.C., and Sundquist, E.T. 1997. Winter CO₂ fluxes in a boreal forest. *J. Geophys. Res.* **102**(D24): 28 795 – 28 804.
- Yin, X., Perry, J.A., and Dixon, R.K. 1989. Fine-root dynamics and biomass distribution in a *Quercus* ecosystem following harvest. *For. Ecol. Manage.* **27**: 159–177.