TRAP: a modelling approach to below-ground carbon allocation in temperate forests

Daniel P. Rasse[1,4], Bernard Longdoz[2] & Reinhart Ceulemans[3]
Université de Liège, Laboratoire de Physique Atmosphérique et Planétaire, 5 Avenue de Cointe, 4000 Liège, Belgium. [2]*Faculté Universitaire des Sciences Agronomiques - Unité de Physique et de Chimie Physique - 8, Avenue de la Faculté - 5030 Gembloux, Belgium.* [3]*University of Antwerp - ULA, Department of Biology, 1 Universiteitsplein, B-2610 Wilrijk, Belgium.* [4]*Corresponding author**

Abstract

Tree root systems, which play a major role in below-ground carbon (C) dynamics, are one of the key research areas for estimating long-term C cycling in forest ecosystems. In addition to regulating major C fluxes in the present conditions, tree root systems potentially hold numerous controls over forest responses to a changing environment. The predominant contribution of tree root systems to below-ground C dynamics has been given little emphasis in forest models. We developed the TRAP model, i.e. Tree Root Allocation of Photosynthates, to predict the partitioning of photosynthates between the fine and coarse root systems of trees among series of soil layers. TRAP simulates root system responses to soil stress factors affecting root growth. Validation data were obtained from two Belgian experimental forests, one mostly composed of beech (*Fagus sylvatica* L.) and the other of Scots pine (*Pinus sylvestris* L.). TRAP accurately predicted ($R = 0.88$) night-time CO_2 fluxes from the beech forest for a 3-year period. Total fine root biomass of beech was predicted within 6% of measured values, and simulation of fine root distribution among soil layers was accurate. Our simulations suggest that increased soil resistance to root penetration due to reduced soil water content during summer droughts is the major mechanism affecting the distribution of root growth among soil layers of temperate Belgian forests. The simulated annual rate of C input to soil litter due to the fine root turnover of the Scots pine was 207 g C m^{-2} yr^{-1}. The TRAP model predicts that fine root turnover is the single most important source of C to the temperate forest soils of Belgium.

Introduction

Estimating below-ground C fluxes in forest ecosystems has become of increasing interest to the scientific community as forest soils are a potential sink for the C released in the atmosphere by fossil fuel consumption. Tree root systems, which play a major role in below-ground C dynamics, are one of the key research areas for estimating long-term C cycling in forest ecosystems. Several studies indicate that about one half of all photosynthetic C is allocated below-ground in forest ecosystems (Beets and Whitehead, 1996; Hendrick and Pregitzer, 1993; Horwath et al., 1994; Malhi et al., 1999). Root respiration and decomposition of recent root exudates and necromass generate more than half of the total CO_2 efflux from forest soils (Ewel et al., 1987; Ruess et al., 1996; Thierron and Laudelout, 1996). For a temperate mixed hardwood forest, Bowden et al. (1993) estimated that 33% of total soil respiration resulted from root respiration and another 30% from root litter decomposition.

In addition to regulating major C fluxes under present conditions, tree root systems potentially hold numerous controls over forest responses to a changing environment. Although the effects of elevated CO_2 on above-ground processes have been incorporated into recent models (Friend et al., 1998), less attention has

been paid to the potential effects of global change on tree root systems. Modifications to the soil temperature regime affect root growth (King et al., 1997; Korotaev, 1989; Kuhns, 1985) and respiration (Zogg et al., 1996). Changes in the soil water regime affect soil aeration (Van Praag and Weissen, 1982) and soil penetrability to roots (Jones et al., 1991), which modify tree root distribution within the soil profile (Adamczyk and Fajto, 1987). Ryan et al. (1996) suggest that exudation from fine roots is increased when soil conditions are less conducive to root growth. Therefore, there is a need to model tree root system responses to soil stress in order to predict below-ground C cycling under future environmental conditions in the course of the next century.

The predominant contribution of tree root systems to below-ground C dynamics has been given little emphasis in forest models. This lack of attention to below-ground C allocation in most models has historically been driven by the scarcity of available data (Raich and Nadelhoffer, 1989). This situation has somewhat changed in the last decade as more studies were conducted on root respiration and below-ground C allocation. The first objective of this research was to develop the TRAP model, i.e. Tree Root Allocation of Photosynthates, which describes the fate of the photosynthetic C allocated to tree root systems as a function of soil stress factors including temperature, penetrability, aeration and acidity. The second objective was to use TRAP to evaluate the contribution of tree root systems to long-term C fluxes in temperate forests.

Model description

General structure of the TRAP model

TRAP is a mechanistic model developed for predicting the partitioning of photosynthates between fine and coarse roots of trees among a series of user-defined soil layers, and the fate of these photosynthates as they are allocated to maintenance respiration, growth respiration, growth, C loss due to soil stress factors and litter production. Carbon reservoirs of (1) fine roots, (2) coarse roots, (3) litter and (4) soil organic matter are computed at each time step by solving all differential equations defined between incoming and outgoing C fluxes. All C reservoirs are computed several times per day at a frequency defined by the time step of the input weather data. For the simulations reported in this study, weather data were collected every 30 min.

Although the integration time step is short, TRAP is designed to simulate the evolution of C reservoirs over periods longer than a century. Forests of any age, i.e. from seedlings to mature stands, can be used as initial conditions for the model, which will further simulate root growth and evolution of litter and soil organic C reservoirs. TRAP simulates soil stress factors affecting (1) the vertical growth rate of the coarse root system, (2) the allocation of C to fine roots among soil layers, (3) the increased loss of carbon by fine roots when growing in a stressed environment, representing the combined effects of increased growth respiration cost and exudation.

TRAP, which is a below-ground carbon allocation model, needs to be coupled to an assimilate-production model for simulating at every time step the amount of photosynthates available to below-ground organs. For this purpose, we used the ASPECTS model which simulates tree growth and C fluxes in temperate forests (Rasse et al., 2000). ASPECTS computes rates of photosynthesis according to the theoretical model of De Pury and Farquhar (1997) and stomatal conductance according to the semi-empirical model of Leuning (1995). In ASPECTS, soil water content is computed for a series of user-defined soil layers. The net flux of water between two adjacent soil horizons is computed by solving the equation of Richards for unsaturated flow, according to the methodology of Viterbo and Beljaars (1995). The relationship between the volumetric water content (θ) of each layer and its pressure head, as well as the hydraulic conductivity, are parameterised according to Saxton et al. (1986). The bottom water flow boundary condition is free drainage, i.e. $\partial\theta\partial z = 0$, where z is the depth. Evaporation from the soil surface which defines the upper boundary condition was computed according to the methodology of Mahfouf and Noilhan (1991). ASPECTS also simulates soil temperature for each soil layer by solving the heat diffusion equation, with a bottom boundary condition set to zero heat flux, and an upper boundary condition defined by equating soil surface temperature to air temperature.

Soil stress

The TRAP model simulates four soil stress factors affecting root growth and distribution: (1) temperature, (2) soil strength, which limits soil penetrability to roots, (3) aeration and (4) acidity. Water stress is taken into account as a component of soil strength stress, which is a function of soil water content and

bulk density. In addition, water stress has a negative feedback on stomatal conductance. Severity of each soil stress factor affecting each soil layer is ranked from 0.00, i.e. absence of stress, to 1.00, i.e. maximum stress. Total soil stress affecting root growth in each soil layer (*Rstress*) is taken as the largest of the four stress factors, as suggested by Jones et al. (1991).

Temperature stress prevents root growth below a species-specific base temperature and above a maximum temperature. Optimum temperature for root growth is taken as the average of minimum and maximum temperatures. Because the rate of root growth is near maximum on a range of temperature around the optimum temperature, a sine function was chosen to describe temperature stress for root growth, as suggested by Jones et al. (1991). For each soil layer, temperature stress between base and maximum temperatures is computed as follows:

$$T_{\text{stress}} = \sin\left({}^{1.57 \times (T_{\text{soil}} - T_{\text{base}})}/_{(T_{\text{opt}} - T_{\text{base}})} \right) \tag{1}$$

where, T_{soil} is the temperature (°C) of the each soil layer, T_{base} is the species-specific base temperature (°C) for root growth, and T_{opt} is the species-specific optimum temperature (°C) for root growth. Base temperature for most temperate tree species approximates 5 °C (Korotaev, 1989; Lopushinsky and Max, 1990). Temperature thresholds for root growth are in Table 1.

Root sensitivity to soil strength was simulated in TRAP according to the model presented by Jones et al. (1991). Soil strength stress to root growth is a function of tree species, soil texture, bulk density and soil moisture content. Maximum bulk density allowing root growth (BD_{max}) is computed as follows:

$$BD_{\text{max}} = BD_{\text{coef}} + (0.04 \times \text{sand}) \tag{2}$$

where, BD_{coef} is the species-specific coefficient of root sensitivity to soil strength (Mg m^{-3}), and sand is the percentage of sand in the soil layer (%). Literature-derived BD_{coef} values for beech and Scots pine are 1.55 and 1.62 Mg m^{-3}, respectively (Table 1). Soil strength stress decreases linearly from BD_{max} to an optimal bulk density (BD_{opt}) below which soil strength does not limit root growth. If $BD_{max} \geq BD \geq BD_{opt}$:

$$BD_{\text{stress}} = (BD_{\text{max}} - BD)/_{(BD_{\text{max}} - BD_{\text{opt}})} \tag{3}$$

where, BD is the bulk density of the soil layer (Mg m^{-3}), BD_{stress} is the component of the soil strength stress attributable to BD. Optimal bulk density is computed according to the following generic formula:

$$BD_{\text{opt}} = 1.3 + (0.005 \times \text{sand}) \tag{4}$$

Drying of soils increases soil strength. At a given BD, root growth is maximum at the drained upper limit (DUL) and minimum at the lower limit (LL) of plant-extractable water. Because incipient drying of soils at the DUL modifies slowly the soil strength stress, Jones et al. (1991) chose a sine function to describe the effects of soil drying on soil strength.

$$ST_{\text{stress}} = BD_{\text{stress}} \times \sin\left({}^{(\text{SWC} - \text{LL})}/_{(\text{DUL} - \text{LL})} \right) \tag{5}$$

where, ST_{stress} is the soil strength stress (dimensionless), and SWC is the volumetric soil water content (%).

Tree-root colonization of soil profiles is limited by the amount of oxygen available to root respiration. Jones et al. (1991) used the concept of critical porosity (POR_{crit}), which is the ratio of soil water to total soil porosity above which root growth is impeded. POR_{crit} is species-specific and depends on soil texture:

$$POR_{\text{crit}} = POR_{\text{species}} + (0.4 \times \text{clay}) \tag{6}$$

where, POR_{species} is the species-specific coefficient (%), and clay is the clay content of the soil layer (%). Above POR_{crit}, aeration stress (AIR_{stress}) is computed as a linear function of the ratio water filled porosity-total porosity (POR_{w}):

$$AIR_{\text{stress}} = {}^{(1 - POR_{\text{w}})}/_{(1 - POR_{\text{crit}})} \tag{7}$$

Soil acidity is treated as a static stress by the TRAP model, which does not simulate modifications of soil chemistry in response to environmental changes. Acidity stress is generally expressed in terms of aluminium toxicity or pH (Nosko and Kershaw, 1992). In TRAP, we opted for a simple acidity-stress module based on pH. This practical choice was guided by the availability of information for beech and Scots pine regarding their sensitivity to soil pH (Table 1). Four pH thresholds were identified for each tree species: (1) lowest pH at which root growth occurs, (2) lowest pH at which root growth is optimum, (3) highest pH at which root growth is optimum and (4) highest pH at which root growth occurs. No acidity stress is simulated between the two optimum thresholds. The acidity stress increases linearly from these optima to the lowest and highest pH allowing root growth.

Table 1. List of model parameters

Parameters	Beech	Scots pine	Source
Optimum temperature for root growth (°C)	19.4	16.5	Korotaev (1989)
Minimum temperature for root growth (°C)	5.0	5.0	Korotaez (1989), Lopushinsky and Max
Bulk density coefficient (BD_{coef}, Mg m^{-3})	1.55	1.62	estimated from Korotaev (1992) and Weissen (1991)
Critical % of water-filled porosity ($POR_{species}$ %)	0.4	0.7	estimated from Weissen (1991)
Minimum pH allowing root growth	3.75	2.25	Weissen (1991)
Minimum pH for optimum root growth	4.25	3.75	Weissen (1991)
Maximum pH for optimum root growth	8.25	5.75	Weissen (1991)
Maximum pH allowing root growth	9.25	7.75	Weisen (1991)
Coarse root tunrover rate (yr^{-1})	0.02	0.02	Kurz et al. (1996)
Fine root turnover rate (yr^{-1})	1.0	1.0	Hoffmann (1995)
Allocation coefficient for above-ground organs (dimensionless)	0.47	0.47	estimated from Lee et al. (1998), Janssens et al. (1999) and Laitat et al. (1999)
Allocation coef. for starch (dimensionless)	0.10	0.00	calibrated
Proportion of below-ground assimilates allocated to fine roots:			
(1) leaf expansion phase (%)	100	100	Lüdeke et al. (1994)
(2) rest of the growing season (%)	75	75	calibrated
Vertical growth coefficient for coarse roots (Vcoef, m yr^{-1})	0.15	0.15	calibrated
Partitioning coef. between fine root C loss and redistribution (β, dimensionless)	0.5	0.5	default value in the absence of literature data
Maintenance respiration coefficient (α d^{-1}):			
(1) fine roots	$6\ 10^{-4}$	$6\ 10^{-4}$	Rasse et al. (2001)
(2) coarse roots	$2\ 10^{-4}$	$2\ 10^{-4}$	Rasse et al. (2001)
Proportion of growth respiration to growth (%)	20	20	Hoffman (1995)

Carbon allocation

The fraction of photosynthates allocated to below-ground organs (BG_{frac}) is computed according to the following formula:

$$BG_{frac} = 1.0 - AG_{frac} - STA_{frac} \qquad (8)$$

where, AG_{frac} is the fraction of assimilates allocated to above-ground organs, and STA_{frac} is the fraction of assimilates allocated to the starch reserve. We compiled literature data about root–shoot ratios of temperate trees from saplings to mature stands (Janssens et al., 1999; Laitat et al., 1999; Lee et al., 1998) to determine the dependency of AG_{frac} on stand age:

$$AG_{frac} = 0.47 \times (1.0 - \exp(-(2.0 + age)/5.0)) \tag{9}$$

where, age is the age of the stand in years. Given that the starch fraction is used to restart leaf growth of deciduous trees in the spring, STA_{frac} is set to 0.00 for Scots pines at all time. For beech, STA_{frac} is set to 0.00 during the leaf shooting phase, and 0.10 during the rest of the growing season.

Photosynthates allocated to roots are partitioned between the coarse and the fine root systems according to phenological phases. During the leaf expansion phase in the spring, all below-ground assimilates are allocated to the fine roots, as suggested by Lüdeke et al. (1994). During the rest of the year, 75% of below-ground assimilates are allocated to the fine root system, and the remaining 25% to the coarse root system.

The TRAP model simulates tree growth from seedlings to mature trees, which requires a variable depth of the coarse root system. The potential downward expansion rate of the coarse root system is calculated as a linear function of stand age. This potential growth rate is decreased by soil stresses, so that the actual downward expansion rate through the lth soil layer (Vcr_l) is given by:

$$Vcr_l = Vcoef \times ((100 - age)/100) \times Rstress_l$$
$$, age \leq 100 \tag{10}$$

$$Vcr_l = 0.0 \qquad , age > 100 \tag{11}$$

where, Vcoef is the Vcr for 1-year old saplings in unstressed conditions, and $Rstress_l$ is the total soil stress affecting root growth in the lth soil layer where the root front is located.

In TRAP, the volume of soil explored by the coarse root system is represented by a downward-pointing cone. The height of the cone corresponds to the depth of the coarse root system. We further assumed that within this volume of soil, coarse root C distribution is homogeneous. Coarse root assimilates (A_{CR}) are partitioned among soil layers following the proportion
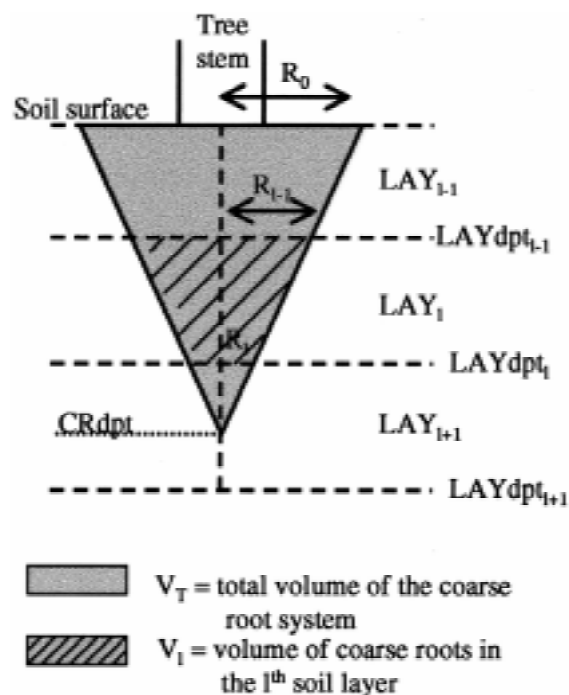

Figure 1. Schematic diagram of coarse root allocation within the soil profile, where R_l is the lateral extent of the coarse root system at the upper limit of the lth soil layer, CRdpt is the depth of the coarse root system, and LAYdpt is the depth of the lth soil layer.

of root C contained in each soil layer:

$$\Delta CR_l = A_{CR} \times CRprop_l \tag{12}$$

where ΔCR_l is the amount of assimilates allocated to coarse roots contained in the lth soil layer, and $CRprop_l$ is the fraction of A_{CR} allocated to the lth soil layer. As coarse root density is considered homogeneous, $CRprop_l$ is the ratio between the volume of soil explored by coarse roots in the lth soil layer (V_l) and the total volume of soil explored by the coarse root system (V_T) (Figure 1):

$$CRprop_l = {}^{V_l}/_{V_t} \tag{13}$$

According to the volume of a cone:

$$V_T = {}^{\pi \times R_0^2 \times CRdpt}/_3 \tag{14}$$

where R_0 is the lateral extent of the coarse root system at the soil surface, and CRdpt is the depth of the coarse root system (Figure 1). Following the same formula, V_l is defined by:

$$V_l = \left[{}^{\pi \times R_{l-1}^2 \times (CRdpt - LAYdpt_{l-1})}/3 \right] - \left[{}^{\pi \times R_l^2 \times (CRdpt - LAYdpt_l)}/3 \right] \tag{15}$$

where, and LAYdpt$_l$ is the bottom depth of the lth soil layer. The lateral extent of the coarse root system at the top of the lth and (l+l)th soil layers, i.e. R$_{l-1}$ and R$_l$, respectively, are defined as:

$$R_{l-1} = R_0 \times (CRdpt - LAYdpt_{l-1}) / CRdpt \qquad (16)$$

$$R_l = R_0 \times (CRdpt - LAYdpt_l) / CRdpt \qquad (17)$$

By substituting Equations [16] and [17] in Equation [15], in a first step, and Equations [14] and [15] in Equation [13], in a second step, Equation [13] is rewritten as:

$$CRprop_l = \left((CRdpt - LAYdpt_{l-1})^3 - \right. \qquad (18)$$

$$\left. (CRdpt - LAYdpt_l)^3 \right) / CRdpt^3$$

Allocation of C to the fine root system (A$_{FR}$) is based on the assumption that fine roots develop in the vicinity of existing coarse roots. We assumed that fine roots did not extend below maximum depth of the coarse roots. Vertical distribution of fine root C among soil layers is driven by the vertical density profile of the coarse root system, and the total stress affecting each soil layer. In non-stressed conditions, assimilates are allocated to each soil layer as follows:

$$\Delta FR_{NSl} = A_{FR} \times CR_l / \sum_{l=l}^{nlayer} CR_l \qquad (19)$$

where, ΔFR_{NSl} is the amount of assimilates allocated to fine roots growing in the lth soil layer in non-stressed conditions.

The ASPECTS model simulates two distinct effects of soil stress on the allocation of assimilates to fine roots: (1) a reallocation of assimilates to fine roots growing in soil layers where lower stress conditions prevail, (2) an increase in C losses by fine roots, as suggested by Ryan et al. (1996). Although this increased C loss is probably due to a combination of increases in growth respiration rates and exudation, we assumed in the absence of literature data that all C loss due to soil stress was immediately released as CO_2. Each ΔFR_{NSl} is multiplied by the total stress affecting the corresponding soil layer, which ranges from 0.00 to 1.00. Therefore, when stress factors are larger than 0.00, the total amount of assimilates initially allocated to fine root growth is smaller than A$_{FR}$. A proportion of assimilates, which have not been initially allocated,

is lost as increased root respiration (FRloss):

$$FRloss = \beta \times \left(A_{FR} - \sum_{l=l}^{nlayer} (\Delta FR_{NSl} \times Rstress_l) \right) \qquad (20)$$

The remaining part of the assimilates is redistributed (REDIS) to fine-root growth in the other soil layers:

$$REDIS = (1 - \beta) \times$$
$$\left(A_{FR} - \sum_{l=l}^{nlayer} (\Delta FR_{NSl} \times Rstress_l) \right) \qquad (21)$$

where, β is a dimensionless partitioning coefficient between FRloss and REDIS. In the absence of literature data, we have assumed that $\beta = 0.5$, which implies that FRloss is equal to REDIS. Redistribution of assimilates due to soil stress is conducted according to the weighed averages of soil-stress factors. Therefore, the total amount of assimilates allocated to fine-root growth in each soil layer equals:

$$\Delta FR_l = (\Delta FR_{NSl} \times Rstress_l) +$$
$$\left(REDIS \times Rstress_l / \sum_{l=l}^{nlayer} Rstress_l \right) \qquad (22)$$

The structure of the TRAP model for the partitioning and allocation of assimilated C to fine and coarse roots within a series of soil layers was summarised in Table 2.

Maintenance respiration costs of the fine and coarse root systems are computed according to the function suggested by Zogg et al. (1996):

$$Rm = C_{res} \times f_{live} \times a \times N \times e^{0.1 \times T} \qquad (23)$$

where, Rm is the maintenance respiration (g m^{-2} d^{-1}), C$_{res}$ is the total C content of the coarse or the fine root system (g m^{-2}), f$_{live}$ is the fraction of live tissue to total biomass (f$_{live}$ = 1 for fine roots, f$_{live}$ = sapwood fraction of coarse roots), α is the coefficient for maintenance respiration (d^{-1}), N is the nitrogen concentration (% of dry matter), and T is the soil temperature of the soil layer for which root respiration is computed (°C). The α coefficient of fine roots was chosen as three times that of coarse roots. This ratio was based on comparisons reported by Ryan (1991) and Ryan et al. (1996) between the respiration of fine roots and that of other plant tissues. We have shown in another study that α approximates 0.0002 for Belgian

Table 2. Summary of the TRAP model structure for the partitioning and allocation of assimilated C to fine and coarse roots within a series of soil layers

Successive steps for C partitioning and allocation to roots	Controlling factors and mechanisms
Partitioning of assimilates to below-ground organs	Function of stand age, phenological phase and tree species (Equations 8 and 9)
Partitioning of below-ground assimilates between fine and coarse root systems	Function of the phenological phase (100% to fine roots during the leaf expansion phase, 75% during the rest of the year)
Partitioning of coarse root assimilates among soil layers	(a) According to a homogeneous conical distribution (Equations 12–18). (b) Function of the depth of the coarse root system, which is a function of stand age and (Equations 10 and 11) and soil stress (Equations 1–7)
Partitioning of fine root assimilates among soil layers (Equation 22)	(a) According to the distribution of the coarse root system (b) Considering root C loss associated with soil stress (Equation 20, and Equations 1–7) (c) Considering redistribution of assimilates among soil layers due to soil stress (Equation 21, and Equations 1–7)
In each soil layer, allocation of fine and coarse root assimilates to growth and respiration	(a) Maintenance respiration costs are a function of soil temperature, root N content, and fraction of live to total tissue biomass (Equation 23) (b) Growth respiration: 20% of remaining growth assimilates.

forest ecosystems (Rasse et al., 2001). Growth respiration is computed as 20% of A_{CR} and A_{FR} allocated to each soil layer, as suggested by Hoffmann (1995). Therefore, total respiration of the fine root system is the sum of (1) the increased C loss due to soil stress, (2) maintenance respiration and (3) growth respiration.

Litter production and decomposition

The TRAP model simulates the turnover of fine and coarse roots, which generates C inputs to litter pools of the corresponding soil layers. The litter pool of the upper soil layer receives contributions from leaves and branches in addition to roots, while litter pools of deeper soil layers are solely composed of root debris. Published values for fine root turnover rates fluctuate between 0.33 and 3 yr^{-1} (Steele et al., 1997), although most studies report turnover rates close to 1 yr^{-1} (Fahey and Hughes, 1997; Harris et al., 1977; Usman et al., 1997). As the life span of fine roots is somewhat uncertain, we opted for a turnover rate of 1 yr^{-1}, as suggested by Hoffmann (1995). Very few estimates of coarse root turnover rates are available in the literature. Fine and coarse root turnover rates are modified by the diameter class which separates fine roots from coarse

roots. In the literature, fine roots have been defined as less than 1, 2 or 5 mm in diameter (Janssens et al., 1999; Steele et al., 1997). The smaller the diameter of roots, the faster their turnover rate. Therefore, the coarse root turnover rate increases when the diameter separating fine roots from coarse roots is reduced. In this study we opted for a coarse root (i.e. > 1 mm) turnover of 0.02 yr^{-1}, as suggested by Kurz et al. (1996). In addition to the simulation of a continuous root turnover, production of root litter is also simulated at thinning. Hence, the ASPECTS model in which TRAP has been implemented simulates thinning of the forest (Rasse et al., 2001). Carbon contained in fine and coarse roots of cut trees is allocated to the soil litter pools of the corresponding soil layers. In addition, carbon contained in leaves and branches is allocated to the litter pool of the upper soil layer. We assumed that stems are removed from the plots at harvest, leaving no stem C to the litter pool of the upper soil layer.

Litter decomposition is calculated as a simple function of soil water content, temperature and pH. Litter decomposition is optimal at field capacity and decreases at low soil water contents due to the lack of available water, and at high soil water contents due to anaerobiosis. Temperature dependence of litter de-

composition is described in TRAP according to the equation of Nemry et al. (1996):

$$f(T) = 1.84^{(T/10)} \qquad (24)$$

where, $f(T)$ is the temperature dependence of litter decomposition, and T is the temperature of a given soil layer (°C).

Materials and methods

Experimental data

Validation data were obtained from two Belgian experimental forests located at Vielsalm (50° 17′N, 6° 00′ E), and Brasschaat (51° 18′ N, 4° 31′ E), respectively. General characteristics of these experimental sites are summarised in Table 3. The Vielsalm forest plot, covering 8000 m², is mostly composed of beech planted in 1908 for two thirds of the area and of Douglas fir (*Pseudotsuga mensiezii* Mirb.) in the rest of the area. Biomass measurements were conducted in 1998 by harvesting four beech trees from the forestplot. Published allometric relationships were calibrated with the biomass measurements and applied to the entire tree population of the research plot to derive coarse root biomass, as described by Lefèvre et al. (1999). Fine root biomass was estimated from auger sampling conducted in 1997. The forest plot was sampled at 50 random locations to a depth of 90 cm. Each sample was then divided in 15-cm layers. Roots were washed free of soil, oven-dried at 70 °C and weighed. All plant tissues were analysed for total C and N. Detailed materials and methods for biomass, C and N measurements at the Vielsalm site have been given by Laitat et al. (1999).

The Brasschaat forest plot is mostly composed of Scots pines planted in 1929. The research site is located in a 150 ha mixed coniferous/deciduous forest. Coarse root systems of four trees were excavated in 1995 to establish site-specific allometric relationships between diameter at breast height (DBH) and coarse roots. Regressions between coarse roots and DBH were used to scale up to the stand level. Fine roots were sampled at 30 locations in the forest plot in 1997. As for the Vielsalm site, each sample was then divided in 15-cm layers. Roots were washed free of soil, oven-dried at 70 °C and weighed. Carbon and N contents of plant tissue were determined using the dry combustion technique. Detailed materials and methods for plot management, biomass measurements and C analyses

Table 3. Description of the two experimental forest sites in Belgium

	Vielsalm	Brasschaat
Dominant species	Beech	Scots pine
Year of planting	1908	1929
Mean annual precipitation (mm)	972	767
Mean annual temperature (°C)	7.5	9.8
Elevation (m)	490	16
Soil type FAO Class.	Dystric Cambisol	Haplic Podzol
Soil Texture	Silt loam	Sandy
Soil pH (H_2O)	≈ 4.0	3.8–4.1
Soil depth (m)	1.25	1.00

have been given by Cermák et al. (1998) and Janssens et al. (1999).

Weather data for model inputs were measured on top of 40-m high instrumented towers located at both experimental sites. Data sets consisted of half-hourly measurements of: (1) air temperature, (2) incoming solar radiation, (3) precipitation, (4) relative humidity, (5) wind speed and (6) atmospheric pressure. Weather data were available from August 1997 to July 1999 at Vielsalm, and from January 1997 to December 1998 at Brasschaat. At the Vielsalm site, the CO_2 fluxes exchanged by the forest were measured continuously using the eddy covariance method. A common methodology for the measurement and data treatment, set up within the frame of the EUROFLUX network, was used (Aubinet et al., 2000). Vielsalm CO_2 flux data were available for the same period as weather data. Respiration of the forest ecosystem was estimated from the night-time CO_2 fluxes, as suggested by Baldocchi et al. (1997). In addition, direct measurements of soil CO_2 efflux were conducted by close-dynamic-chamber system on 29 spots of the Vielsalm forest from August 1997 to August 1999, as described by Longdoz et al. (2000).

Results

Simulated total stress to root growth in the upper 15-cm soil profile displayed large fluctuations during 1997 and 1998 at Vielsalm (Figure 2). The upper soil profile was chosen as an example for this analysis because variations in stress factors during the year are
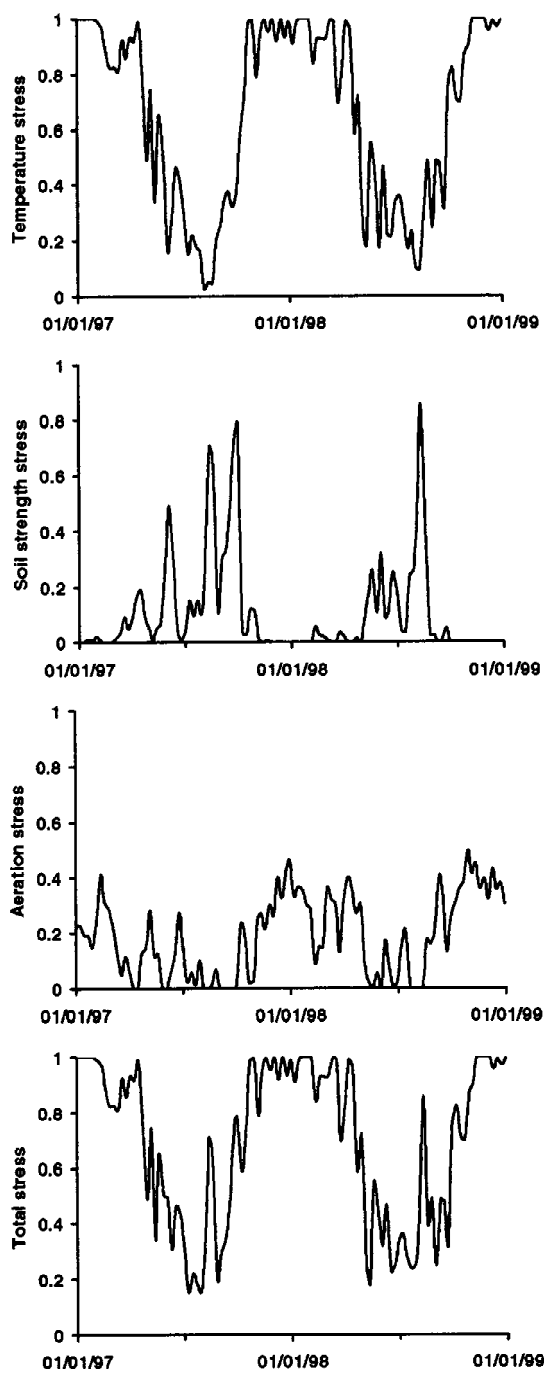
Figure 2. Simulated soil stress factors to beech root growth in the upper 15-cm soil profile at the Vielsalm experimental forest site in 1997 and 1998. All stress factors are expressed on a relative scale from 0 to 1.

most pronounced at the soil surface. Winter temperatures were often below the minimum threshold for root growth (Figure 2). As the soil warmed up in the
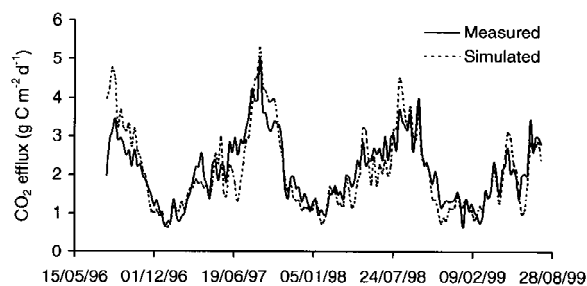

Figure 3. Simulated versus measured night-time CO_2 efflux rates from the Vielsalm experimental forest from August 1996 to July 1999. Data points are weekly averages.
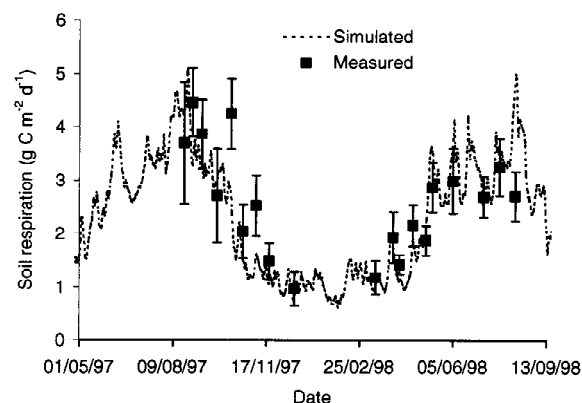
Figure 4. Simulated versus measured soil respiration rates for the Vielsalm experimental forest. Data points are daily averages.

spring, the temperature stress decreased, although it never reached 0 when averaged on a weekly basis. The soil strength stress displayed a few sharp peaks during the warmer season (Figure 2). Little to no soil strength stress was simulated during the cold season. The aeration stress displayed a similar annual pattern as that of the temperature stress, although of much reduced magnitude (Figure 2). As the total stress is computed according to the law of the most limiting factor, anaerobiosis appears to have little impact on root growth in the upper soil profile at Vielsalm. In other words, when aeration is a limiting factor, soil temperature is nearly always limiting to a larger extent.

Night-time CO_2 fluxes from the Vielsalm forest as measured by eddy covariance were accurately simulated ($R = 0.88$) by the TRAP model (Figure 3). This accurate simulation resulted from an excellent prediction of the overall trend of the annual night-time respiration cycle, and from good predictions of weekly variations of the respiration fluxes. Soil respiration rates as measured by close-dynamic-chamber systems were also accurately simulated ($R = 0.77$) by
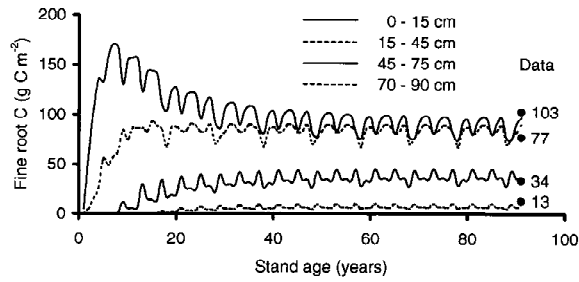
Figure 5. Evolution of simulated fine root carbon reservoirs per soil layer for beech trees during a 90-year period at the Vielsalm experimental forest. Measurements conducted at the research site for 90-year old trees are represented on the right hand side of the graph and are expressed in g C m^{-2}.
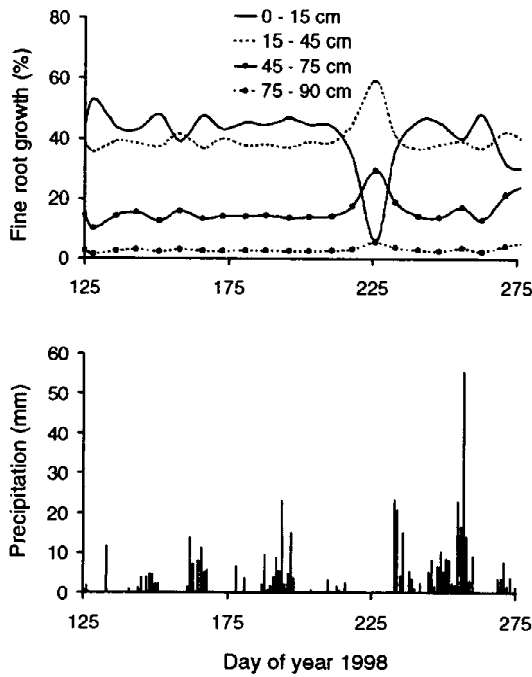

Figure 6. Simulated fine root growth for four soil layers and measured precipitation during the 1998 growing season for the beech experimental forest site at Vielsalm.

Figure 7. Simulated evolution of fine and coarse root carbon reservoirs over a 66-year period of Scots pine growth at the Brasschaat experimental forest. Measurements conducted at the research site for 66-year old trees are represented on the right hand side of the graph and are expressed in g C m^{-2}.

the TRAP model (Figure 4). Most model-estimated values (i.e. 13 out of 17) were within the error bars associated with the measurements.

Total fine root biomass at Vielsalm was predicted within 6% of measured values (Figure 5). The best simulation was obtained for the 45–70-cm soil depth, where simulated values were within 1% of measurements. For the 0–15-cm mineral soil layer, measured and simulated values were 103 and 97 g C m^{-2}, respectively. Nevertheless, the data indicated that another 20 g fine root C m^{-2} were contained in the layer
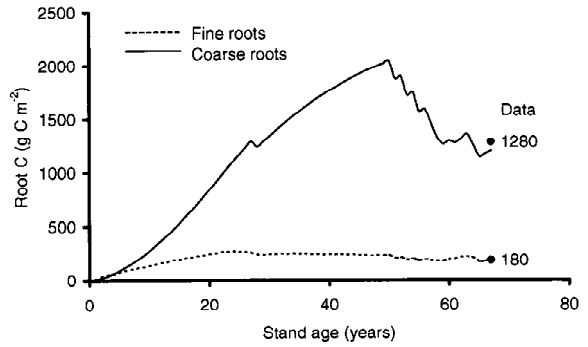
of organic litter covering the soil surface, leading to an 20% underestimation of the total fine root C contained up to a depth of 15 cm in the mineral soil. The TRAP model predicted that the distribution of the fine root system among soil layers changed rapidly for young beech trees, and remained fairly unchanged for trees of 40 years and older. Simulated fine root populations fluctuated on an annual basis, with net production in the spring and summer time, and net root death during winter time. Simulated C allocation to fine root growth among soil layers responded to simulated soil stress. For example, for the 90-year old beeches, the proportion of fine root growth occurring in each soil layer remained fairly constant until a summer drought restricted fine root growth in the uppermost soil layer (Figure 6). The TRAP model predicted that during the drought, a greater proportion of fine root growth occurred in deeper soil layers, which compensated for the restricted root growth in the uppermost soil layer associated with increased soil strength at low soil water contents.

Total fine and coarse root C contents in the soil profile were accurately predicted for the Brasschaat Scots pines, when simulation was conducted from the time of planting in 1929 to the time of root biomass measurements in 1995 (Figure 7). The TRAP model predicted that the total amount of living fine roots reached a plateau approximately 25 years after planting. The multiple sudden drops in the simulated curve of the evolution of coarse root C corresponded to actual thinnings of the stand. The prediction of coarse root C is very sensitive to the simulation of stand thinning, while fine root C was less affected. In agreement with the data, TRAP predicted that about 6–7 times
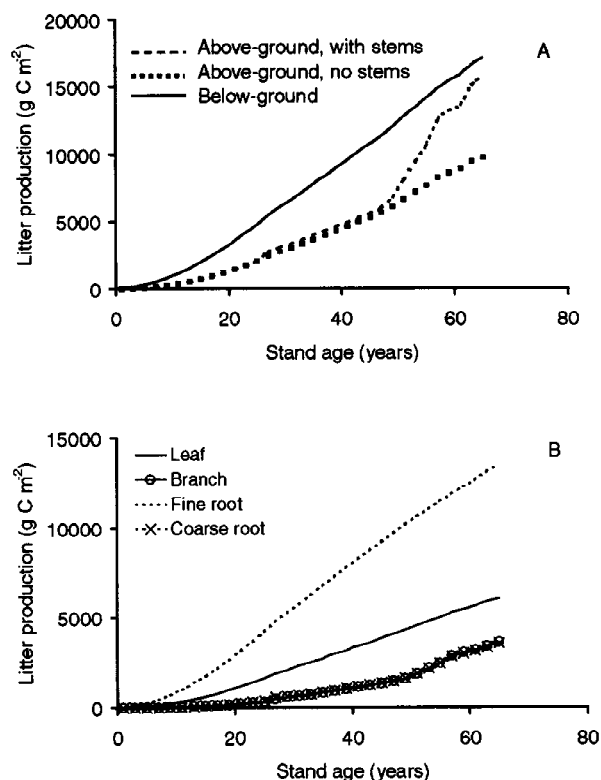
Figure 8. Simulated evolution of the cumulative litter production over a 66-year period of Scots growth at the Brasschaat experimental forest. First, the overall above-pine and below-ground contributions are presented (A). Above-ground litter production was considered with and without stem removal from the forest at stand thinning. Second, the separate contributions of leaves, branches, fine roots and coarse roots are presented (B).

more C is contained in the coarse root system than in the fine root system.

Simulated cumulative litter production during the 66 years of Scots pine growth at Brasschaat was 9700 and 17200 g C m^{-2}, for above- and below-ground organs, respectively (Figure 8A). As previously stated, the TRAP model simulates stem removal from the forest at harvest, leaving no stem C to soil litter pools. Estimated above-ground litter production rises to 15 70O g C m^{-2} when stem C is returned to soil litter pools at harvest. The TRAP model predicted that fine roots generated 79% of the below-ground litter, while coarse root turnover accounted for the remaining 21% (Figure 8B). Simulated branch and coarse root contributions to litter pools were extremely similar. The model suggests that litter contribution by fine roots was more than twice that of needles.

Discussion

The TRAP model predicted that fine root turnover is the single most important source of C to the temperate forest soils examined in this study. The simulated annual rate of C input to soil litter due to fine root turnover at Brasschaat was 207 g C m^{-2} yr^{-1}, when averaged over the 66-year period. Fine root production of temperate forests has been reported to range between 40 and 450 g C m^{-2} yr^{-1} (Fahey and Hughes, 1994; Hendrick and Pregitzer, 1993). Therefore, TRAP estimates are within this range of measured values. Our simulations suggest that the rate of litter accumulation due to fine root production increases from seedlings to 15-year old trees, and remains fairly constant after that (Figure 8). This result was obtained because fine root production is mainly a function of the amount of photosynthates available to below-ground organs. Photosynthate production is directly linked to the leaf area index of the forest stand. Therefore, as the LAI tends towards a plateau at canopy closure, fine root production follows a similar trend. Our simulations of a constant rate of fine root production agrees with results presented by Fahey and Hughes (1994), who measured fine root production rates of 96, 104, 193 and 241 g dry matter m^{-2} yr^{-1} for 2-year old, 3-year old, 4-year old and mature hardwood stands, respectively. Opposite to these results, Vanninen et al. (1996) reported that fine root biomass increases linearly with stand basal area for mature Scots pines.

We simulated a cumulative fine root litter production of 13 700 g C m^{-2}, during the 66 years of Scots pine growth at Brasschaat (Figure 8B), while the measured total phytomass C in the 66-year-old stand was 10 400 g C m^{-2} (Janssens et al., 1999). We therefore estimate that fine root turnover alone produced more C to soil litter than the total amount of phytomass C contained in the stand. The TRAP model correctly predicted that coarse roots contain 6–7 times more C than fine roots for the Brasschaat Scots pine (Figure 7), in agreement with measurements reported by Janssens et al. (1999). The model also predicted that the contribution of coarse roots to the soil C was about four times lower than that of fine roots (Figure 8B). These results agree with the study of Beets and Withehead (1996) who reported that the ratio of fine to coarse root production of *Pinus radiata* ranges from 3 to 10. TRAP simulations also suggest that tree harvest is an important factor driving coarse root litter

production, while little impact is expected on fine root litter production.

The repartition and turnover of fine roots in the soil profile drive C inputs to the different soil layers (Figure 5). This repartition is modified by the depth of the growing coarse root system and by the severity of soil stress factors (Figures 5 and 6). In our simulations, total stress to root growth resulted mainly from temperature stress (Figure 2). Nevertheless, temperature stress mostly happens during the period when deciduous trees are leafless, and evergreens have a much reduced photosynthesis. Therefore, little root growth is expected due to low photosynthate availability at periods when temperature stress is maximum. Our simulations indicate that the reported effect of soil temperature on root growth (Korotaev, 1989; Kuhns, 1995) will mainly modify the distribution of fine root C within the soil profile during spring and fall periods. Therefore, our model suggests that rising soil temperatures in the course of the next century might substantially modify fine root colonisation of the soil profile during fall and spring. Increased soil strength due to reduced soil water content during summer droughts appeared to be the major mechanism affecting the distribution of root growth among soil layers (Figure 6). Based on our simulations, it might be hypothesised that if climate changes in the course of the next century result in prolonged summer droughts, a larger proportion of root C would be allocated deeper in the soil profile. This mechanism will potentially modify the turnover of soil C in response to future climate changes.

Root activities and populations are very tedious to measure, which greatly limits the amount of root data available for the development and validation of root models (Raich and Nadelhoffer, 1989). Especially, time repeated measurements of tree root biomass in natural forests are nearly non-existent. Although we did not have repeated measurements of root biomass in this study, we have proven that TRAP coupled to ASPECTS accurately simulates the evolution of night-time CO_2 fluxes and soil respiration rates (Figures 3 and 4). These night-time CO_2 fluxes themselves directly relate to soil respiration rates, which represent the largest C flux from forest ecosystems to the atmosphere (Law et al., 1999; Malhi et al., 1999). Our accurate simulations of the directly- and indirectly-measured soil respiration rates for a 3-year period suggest that root respiration and root litter decomposition are accurately predicted by TRAP, which reinforces our confidence in the long-term simulations of root growth and root litter production that we have discussed in this study.

References

Adamczyl B and Fajto A 1987 Root systems of the common pine (*Pinus sylvestris* L.) and the pedunculate oak (*Quercus robur* L.) in varied conditions of moisture content and oxygen access in soils of the Niepolomice forest. Acta Agraria Silvestria Ser. Silvestris. 26, 02–21.

Aubinet M, Grelle A, Ibrom A, Rannik U, Moncrieff J, Foken T, Kowalski A S, Martin P H, Berbigier P. Bernhofer C H, Clement R, Elbers J, Granier A, Grünwald T, Morgenstern K., Pilegaard K, Rebmann C, Snijders W, Valentini R and Vesala T 2000 Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Adv. Ecol. Res. 30, 113–175.

Baldocchi D D, Vogel C A and Hall B 1997 Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric. For. Met. 83, 147–170.

Beets P N and Whitehead D 1996 Carbon partitioning in *Pinus radiata* stands in relation to foliage nitrogen status. Tree Physiol. 16, 131–138.

Bowden R D, Nadelhoffer K J, Boone R D, Melillo J M and Garrison J B 1993 Contributions of aboveground litter, belowground litter and root respiration to total soil respiration in a temperate mixed hardwood forest. Can. J. For. Res. 23, 1402–1407.

Cermák J, Riguzzi F and Ceulemans R 1998 Scaling up from the individual tree to the stand level in Scots pine. I. Needle distribution, overall crown and root geometry. Ann. Sci. For. 55, 63–88.

De Pury D G G and Farquhar G D 1997 Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ. 20, 537–557.

Ewel K C, Cropper W P Jr and Gholz H L 1987 Soil CO_2 evolution in Florida slash pine plantations. II. Importance of root respiration. Can. J. For. Res. 17, 330–333.

Fahey T J and Hughes J W 1994 Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. J. Ecology 82, 533–548.

Friend A, Kellomäki S and Kruijt B 1998 Modelling leaf, tree and forest responses to increasing atmospheric CO_2 and temperature. *In* European Forests and Global Change: The Likely Impacts of Rising CO_2 and Temperature. Ed. PG Jarvis. pp 293–334. Cambridge University Press, Cambridge, UK.

Harris W F, Kinerson R S Jr and Edwards N T 1977 Comparison of belowground biomass of natural deciduous forest and loblolly pine plantations. Pedobiologia 17, 369–381.

Hendrick R L and Pregitzer K S 1993 The dynamics of fine root length, biomass and nitrogen content in two northern hardwood ecosystems. Can. J. For. Res. 23, 2507–2520.

Hoffmann F 1995 FAGUS, a model for growth and development of beech Ecol. Model. 83, 327–348.

Horwath W R, Pregitzer K S and Paul E A 1994 ^{14}C allocation in tree-soil systems. Tree Physiol. 14, 1163–1176.

Janssens I A, Sampson D A, Cermák J, Meiresonne L, Riguzzi F, Overloop S and Ceulemans R 1999 Above- and belowground phytomass and carbon storage in a Belgian Scots pine stand. Ann. For. Sci. 56, 81–90.

Jones A C, Bland W L, Ritchie J T and Williams J R 1991 Simulation of root growth. *In* Modeling Plant and Soil Systems. Eds. J Hanks and JT Ritchie. pp 91–123. Agronomy, 31. American Society of Agronomy. Madison, WI.

King, J S, Thomas R B and Strain B R 1997 Morphology and tissue quality of seedling root systems of *Pinus taeda* and *Pinus ponderosa* as affected by varying CO_2, temperature and nitrogen. Plant Soil 195, 107–119.

Korotaev A A 1989 Investigation of the effect of the soil temperature on the growth and condition of the root systems of young trees. Lesovodstvo, Lesnye Kul'tury i Pochvovedenie 0, 65–69.

Korotaev A A 1992 Effects of soil density on the growth of root systems in tree seedlings. Lesovedenie 0, 74–78.

Kuhns M R 1985 Root growth of black walnut trees related to soil temperature, soil water potential and leaf water potential. For. Sci. 31, 617–629.

Kurz W A, Beukeman 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.

Laitat E, Chermanne B and Portier B 1999 Biomass, carbon and nitrogen allocation in open top chambers under ambient and elevated CO_2 and in a mixed forest stand. A tentative approach for scaling up from the experiments of Vielsalm. *In* Forest Ecosystem Modelling, Upscaling and Remote Sensing. Eds. R Ceulemans, F Veroustraete, V Gond and J Van Rensbergen. pp 33–60. SPB Academic Publishing bv., The Hague, The Netherlands.

Law B E, Ryan M G and Anthoni P M 1999 Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biol. 5, 169–182.

Lee S J, Overdieck D and Jarvis P G 1998 Biomass, growth and carbon allocation. *In* European Forests and Global Change: The Likely Impacts of Rising CO_2 and Temperature. Ed. PJ Jarvis. pp 126–191. Cambridge University Press, Cambridge, UK.

Lefévre F, Laitat E, Medlyn B, Aubinet M and Longdoz B 1999 Carbon pools and annual carbon fluxes in the beech forest sub-plot at the Vielsalm pilot station. *In* Forest Ecosystem Modelling, Upscaling and Remote Sensing. Eds. R Ceulemans, F Veroustraete, V Gond and J Van Rensbergen. pp 137–154. SPB Academic Publishing, The Hague, The Netherlands.

Leuning R 1995 A critical appraisal of a combined stomatal-photosynthesis model for C_3 plants. Plant Cell Environ. 18, 339–355.

Longdoz B, Yernaux M and Aubinet M 2000 Soil CO2 efflux measurements in a mixed forest: Impact of chamber disturbances, spatial variability and seasonal evolution. Global Change Biol. (in press).

Lopushinsky W and Max T A 1990 Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. New For. 4, 107–124.

Lüdeke M K B, Badeck F-W, Otto R D, Häger C, Dönges S, Kindermann J, Würth G, Lang T, Jäkel U, Klaudius A, Ramge P, Habermehl S and Kohlmaier G H 1994 The Frankfurt biosphere model: A global process-oriented model of seasonal and long-term CO_2 exchange between terrestrial ecosystems and the atmosphere. I. Model description and illustrative results for cold deciduous and boreal forests. Clim. Res. 4, 143–166.

Mahfouf J F and Noilhan J 1991 Comparative study of various formulations of evaporation from bare soil using *in situ* data. J. Appl. Meteorol. 30, 1354–1365.

Malhi Y, Baldocchi D D and Jarvis P G 1999 The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. 22, 715–740.

Nemry B, François L, Warnant P, Robinet F and Gérard J-C 1996 The seasonality of the CO_2 exchange between the atmosphere and the land biosphere: A study with a global mechanistic vegetation model. J. Geophys. Res. 101, 7111–7125.

Nosko P and Kershaw K A 1992 The influence of pH on the toxicity of a low concentration of aluminum to white spruce seedlings. Can. J. Bot. 70, 1488–1492.

Raich J W and Nadelhoffer K J 1989 Belowground carbon allocation in forest ecosystems: Global trends. Ecology 70, 1346–1354.

Rasse D R, François L, Aubinet M, Kowalski A S, Vande Walle I, Laitat E and Gérard J-C 2001 Short-term CO_2 fluxes and long-term tree growth in temperate forests: An analysis with ASPECTS. Ecol. Model. (in press)

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

Ryan M G 1991 Effects of climate change on plant respiration. Ecol. Appl. 1, 157–167.

Ryan M G, Hubbard R M, Pongracic S, Raison R J and McMurtrie R E 1996 Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol. 16, 333–343.

Saxton K E, Rawls W J, Romberger J S and Papendick R I 1986 Estimating generalized soil-water characteristics from texture. Soil. Sci. Soc. Am. J. 50, 1031–1036.

Steele S J, Gower S T, Vogel J G and Norman J M 1997 Root mass, net primary productivity and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17, 576–587.

Thierron V and Laudelout H 1996 Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. Can. J. For. Res. 26, 1142–1148.

Usman S, Rawat Y S, Singh S P and Garkoti S C 1997 Fine root biomass production and turnover in evergreen forests of Central Himalaya, India. Oecologia Montana 5, 4–8.

Vanninen P, Ylitalo H, Sievänen R and Mäkelä A 1996 Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). Trees 10, 231–238.

Van Praag H J and Weissen F 1982 Functional aspects and ecology of hydromorphic forest soils. Pedologie 32, 273–284.

Viterbo P and Beljaars C M 1995 An improved land surface parametrization scheme in the ECHWF model and its validation. J. Clim. 8, 2716–2748.

Weissen F 1991 Le fichier écologique des essences. Part 2. Ministère de la Région Wallonne. Namur, Belgique. 190 p.

Zogg G P, Zak D R, Burton A J and Pregitzer K S 1996. Fine root respiration in northern hardwood forests in relation to temperature and nitrogen availability. Tree Physiol. 16, 719–725.

Section editor: G R Shaver