Nitrogen deposition and atmospheric CO₂ interactions on fine root dynamics in temperate forests: a theoretical model analysis

DANIEL P. RASSE
Laboratory of Planetary and Atmospheric Physics, Université de Liège, 5 avenue de Cointe, 4000 Liège, Belgium

Abstract
Fine root turnover is a critical component of below-ground forest ecology, which regulates nutrient dynamics, forest net primary productivity, carbon input to soils, and soil respiration. Understanding fine root responses to changing environmental conditions is critical for predicting the productivity and carbon sequestration potential of forest ecosystems during the 21st century. The first objective of this study is to demonstrate that a mechanistic model can realistically simulate spatial and temporal fine root demography in temperate forests on the basis of two hypotheses: (1) absorption of mineral N (N) stimulates the production of new roots, and (2) fine root longevity decreases with increasing N availability. Based on this model, my second objective is to predict fine root responses to changing atmospheric CO₂ levels and N deposition rates. To meet these objectives, an extensive description of the N cycle and the new fine root module were implemented in the ASPECTS model. In agreement with a wide body of literature information, the new model predicted: (1) a preferential colonisation by fine roots of the uppermost soil layer, and (2) a flush of fine root growth in the spring. The simulations indicate that fine root biomass will increase in response to elevated CO₂ under the double effect of (1) an increase in root longevity due to increased N stress, and (2) larger amounts of assimilates available to the growth of plant tissue due to increased photosynthesis. Although the simulated total fine root biomass increased under both increasing N deposition rates and atmospheric CO₂ concentrations, the model predicts that the distribution of fine roots among soil layers will be altered. This suggests that experimental studies must consider the full depth of the root system in order to accurately assess effects of environmental changes on fine root dynamics. The model also suggests that fine root longevity is a plastic parameter, which varied from less than 1 year to more than 3 years depending on forcing values of N deposition rates and atmospheric CO₂ concentrations. Finally, the model indicates that the increase in net ecosystem exchange (NEE) and soil respiration in temperate forests under elevated CO₂ will be proportional to the amount of available N, with little to no response in low N conditions and up to +28% for both NEE and soil respiration under the highest deposition rate (7.0 g N m⁻² y⁻¹).

Keywords: atmospheric nitrogen deposition, below-ground allocation, elevated CO₂, root demography, root longevity, soil respiration

Received 2 May 2001; revised version received and accepted 5 October 2001

Introduction
Fine root turnover is a critical component of below-ground forest ecology, which regulates nutrient dynamics (Gill & Jackson 2000), forest net primary productivity (Norby & Jackson 2000), carbon input to soils (Rasse et al., 2001).
At the root system level, three main factors have been suggested to control root longevity: (1) mean annual soil temperature, (2) soil moisture status, and (3) nutrient availability (Gill & Jackson 2000; Pregitzer et al. 2000a). Therefore, when root systems are exposed to soil temperature and moisture conditions favourable to growth, as mostly prevailing in temperate forests, nutrient availability is potentially the key factor regulating root growth and turnover. Numerous studies have demonstrated the substantial impact that nutrient availability has on plant root system growth and development (Samuelson et al. 1991; Bloom et al. 1993; Black et al. 1994; Eisenstat et al. 2000; Zhang et al. 2000). Among these nutrients, N seems prevalent, although effects of other nutrients such as phosphorus have also been reported (Black et al. 1994). Pregitzer et al. (1995) reported that soil mineral N is the most important factor regulating fine root demography in *Populus* trees.

Nitrogen availability has dramatic and somewhat paradoxical effects on plant root systems. On the one hand, numerous studies have reported local proliferation of fine roots when exposed to higher levels of available N (Granato & Raper 1989; Samuelson et al. 1991; Pregitzer et al. 1993; Zhang et al. 2000). On the other hand, increased availability of inorganic N within the soil profile can drastically reduce the root-to-shoot ratio of temperate woody species (Linder & Rook 1984; Ryan et al. 1996; Lee et al. 1998). This apparent paradox can only be reconciled if we assume that fine root longevity is decreased by increasing availability of soil mineral N, which has been demonstrated for both woody and non-woody species (Durieux et al. 1994; Pregitzer et al. 1995; Kubiske et al. 1998). Plants growing in nutrient-poor soils would increase the lifespan of their fine roots to optimise nutrient uptake per unit of fine root, as suggested by Ryser (1996).

Nitrogen demand by a plant is a function of its growth rate. Increased levels of atmospheric CO₂ have been reported to increase photosynthesis of temperate trees, and hence the amount of assimilates available to growth (Lee et al. 1998). Therefore, N demand of temperate trees is expected to rise in the course of the 21st century as the atmospheric CO₂ concentration increases. Because fine root dynamics appear to be highly sensitive to N absorption, a significant interaction is expected between atmospheric CO₂ concentrations and atmospheric N depositions on the control of fine root growth and turnover, as suggested by several authors (Kubiske et al. 1998; Eisenstat et al. 2000). This interaction is potentially the reason why increased partitioning of photosynthates to below-ground organs in response to increased atmospheric CO₂ has not yet been demonstrated at this point, as reported by Norby et al. (1999) and Norby & Jackson (2000).

The first objective of the present study is to demonstrate that a mechanistic model can realistically simulate spatial and temporal fine root demography in temperate forests on the basis of the two hypotheses that: (1) absorption of mineral N stimulates the production of new roots, and (2) fine root longevity decreases with increasing N availability. Based on this model, my second objective is to predict fine root responses to changing atmospheric CO₂ levels and N deposition rates.

**Methods**

*General structure of the ASPECTS model*

This study was conducted with a modified version of the ASPECTS model, which is a mechanistic model originally designed to predict the evolution of carbon and water fluxes and reservoirs in temperate forest ecosystems (Misson et al. 2001; Rasse et al. 2001a). I added a comprehensive N cycle to ASPECTS in order to study the interactions between root growth and N uptake, and implemented a novel approach to fine root production and turnover.

ASPECTS is a mechanistic model which computes the evolution of carbon and water reservoirs by solving all differential equations defined between incoming and outgoing carbon and water fluxes (Rasse et al. 2001a). Carbon reservoirs are: (1) sucrose (2) foliage, (3) branches (4) stems, (5) coarse roots, (6) fine roots, (7) soil litter, and (8) soil organic matter (SOM). Water reservoirs are: (1) snow cover, and (2) soil water content per soil layer. Although the integration time step is short, i.e. 60 min in this study, ASPECTS is designed to simulate the evolution of carbon and water reservoirs over periods longer than a century. Initial conditions are defined for forests of any age, i.e. from seedlings to mature stands, and ASPECTS further simulates tree growth and evolution of carbon reservoirs.

ASPECTS simulates four phenological phases for deciduous trees: (1) winter, no photosynthesis, (2) leaf expansion in the spring, (3) wood production during summer and early fall, and (4) leaf senescence. Bud burst is triggered when degree-days accumulated since February 10 over a base temperature of 5 °C reach a thermal time requirement specific to each tree species, as proposed by Hoffman (1995). End of leaf growth is simulated when the leaf area index (LAI) reaches a maximum value defined by an allometric relationship between maximum leaf biomass and wood biomass.

ASPECTS computes rates of photosynthesis according to a modified version of the theoretical model of de Pury &
Farquhar (1997), which is a big-leaf model with a separate integration of sunlit- and shaded-leaf photosynthesis. Canopy photosynthetic capacity results from the integration of the leaf photosynthetic capacity over the entire canopy. Within the photosynthesis sub-model, stomatal conductance is computed by the semi-empirical model of Leuning (1995), which relates stomatal conductance to (1) the net assimilation, (2) the CO₂ concentration at the leaf surface, and (3) the water vapour pressure deficit. In addition, a feedback of soil water stress on stomatal conductance has been introduced (Misson et al. 2001). Maintenance respiration costs are computed for each plant organ according to a generalised version of the equation proposed by Zogg et al. (1996), which relates maintenance respiration to the total carbon content of each plant organ, the fraction of living tissue for the reservoir, the N concentration, and plant tissue temperature. Growth respiration is computed as 20% of growth assimilates allocated to each reservoir, as suggested by Hoffman (1995). Photosynthesis and respiration subroutines of ASPECTS were described by Rasse et al. (2001a).

Photosynthetically fixed carbon is stored in the sucrose pool. This pool regulates carbon allocation to plant organs, and is necessary because ASPECTS computes photosynthesis at short time steps. Sucrose (SU) is allocated to tree organs to satisfy their need for maintenance respiration and growth, which includes both biomass increment and growth respiration. For this modelling study, the allocation subroutine was modified as compared to the original ASPECT version of Rasse et al. (2001a). Hence, the original version of ASPECTS was mainly aimed at describing ecosystem CO₂ fluxes and described assimilate allocation as photosynthesis driven, i.e. source driven. For the present study, numerous sensitivity analyses led me to the conclusion that a sink-driven assimilate approach is necessary to describe organ growth responses to environmental factors, i.e. fine root growth as a function of N uptake in this case. Consequently, the total assimilate demand for maintenance respiration and growth-related processes was computed for each organ at each time step, and entirely met by assimilates allocated from the sucrose pool. Organ demand, except for foliage in spring time, was made a function of the total amount of assimilates in the sucrose pool, as later explained for fine roots in this paper. This implies that assimilate demand by tree organs is regulated in this new version of ASPECTS by the long-term accumulation of sucrose in SU, rather than by short-term photosynthetic rates.

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 & Beljaars (1995). The bottom water flow boundary condition is free drainage, i.e. \( \frac{\partial \theta}{\partial z} = 0 \), where \( z \) is the depth. Evaporation from the soil surface which defines the upper boundary condition was computed according to the methodology of Mahfouf & Noilhan (1991). The total uptake of water by the tree, which is simulated in the photosynthesis and stomatal conductance subroutines, is distributed among the various soil layers according to the root density and the water and aeration stresses of each individual layer. 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. The hydrological subroutines of ASPECTS were described in detail by Misson et al. (2001).

Model structure for the N cycle

Nitrogen uptake by fine roots, which is a driving parameter for this novel approach to fine root dynamics modelling, results from the combined effects of tree N demand and N uptake potential by fine roots. Therefore, these two elements of the N cycle will receive the most attention in the following sections, while other elements of the N cycle will be more briefly exposed. Variable description and units for the following sections are in Table 1. Values and sources for model coefficients are in Table 2.

Tree N demand

Nitrogen demand by tree organs (ORNdem) is a function of organ-specific optimum C/N ratios

\[
ORN_{dem} = ORC \times \left( \frac{1}{ORC_{op}} - \frac{1}{ORC_{N}} \right)
\]

where ORC is organ carbon content of any of the five-tree organs, i.e. foliage (FL), branches (BR), stems (ST), fine roots (FR) and coarse roots (CR), ORC_{op} is the optimum C/N ratio, and ORC_{N} is the organ C/N ratio. Tree N demand (TRNdem) is computed as the sum of organ demands during each phenological phase. I assumed that during the leaf expansion phase in the spring, N is exclusively allocated to growing leaves and fine roots.

Nitrogen is translocated from the N reserve (RESN) to any organ whenever the C/N ratio of this organ surpasses its optimum value. Because organ growth, i.e. carbon accumulation, is potentially simulated at every time step, N is also potentially allocated to the different organs at every time step to maintain the optimum C/N ratio. The maximum value of the N reserve (RESmax) is defined as a proportion of the total tree N (Table 2). A minimum value of the N reserve was defined in ASPECTS, so that deciduous trees keep sufficient N supplies to restart leaf growth in the spring. In the absence of literature data, this quantity was assumed equal to the N amount retranslocated from the leaves to the N reserve at...
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>age</td>
<td>stand age</td>
<td>y</td>
</tr>
<tr>
<td>b</td>
<td>solute buffer power</td>
<td>dimensionless</td>
</tr>
<tr>
<td>Cl</td>
<td>solute concentration in the bulk soil</td>
<td>mol cm$^{-3}$</td>
</tr>
<tr>
<td>Cia</td>
<td>solute concentration at the root surface</td>
<td>mol cm$^{-3}$</td>
</tr>
<tr>
<td>Crati</td>
<td>proportion of the lth soil layer accessible to fine roots</td>
<td>dimensionless</td>
</tr>
<tr>
<td>Chlki</td>
<td>thickness of a soil layer l colonised by roots</td>
<td>m</td>
</tr>
<tr>
<td>D</td>
<td>solute diffusion coefficient in soils</td>
<td>cm$^2$ s$^{-1}$</td>
</tr>
<tr>
<td>DF</td>
<td>solute inflow rate per unit root length</td>
<td>mol cm$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>DF_l</td>
<td>diffusion flow of solute into fine roots of the lth layer</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>Dl</td>
<td>solute diffusion in free solution</td>
<td>cm$^2$ s$^{-1}$</td>
</tr>
<tr>
<td>FRCai</td>
<td>assimilate allocation to fine roots of the lth layer</td>
<td>g C m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>FRCd</td>
<td>fine root C density</td>
<td>g C cm$^{-3}$ FR</td>
</tr>
<tr>
<td>FCN</td>
<td>C/N ratio of fine roots</td>
<td>dimensionless</td>
</tr>
<tr>
<td>FRNopi</td>
<td>optimum C/N ratio of fine roots</td>
<td>dimensionless</td>
</tr>
<tr>
<td>FRC</td>
<td>the fine root carbon content of the lth soil layer</td>
<td>g C m$^{-2}$</td>
</tr>
<tr>
<td>I</td>
<td>potential N inflow rate in fine roots of the lth soil layer</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>L</td>
<td>lifespan of the fine roots</td>
<td>year</td>
</tr>
<tr>
<td>MF_l</td>
<td>mass flow of solute into fine roots of the lth layer</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>MOBNav</td>
<td>mobilisation rate of the available N reserve</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>NH4_l</td>
<td>NH$_4^+$ content of the lth layer</td>
<td>g N m$^{-2}$</td>
</tr>
<tr>
<td>Nmn</td>
<td>minimum soil N concentration for absorption by roots</td>
<td>g N m$^{-3}$</td>
</tr>
<tr>
<td>NO3_l</td>
<td>NO$_3^-$ content of the lth layer</td>
<td>g N m$^{-2}$</td>
</tr>
<tr>
<td>Nsup_l</td>
<td>maximum supply of soil nitrogen in each soil layer</td>
<td>g N m$^{-2}$</td>
</tr>
<tr>
<td>Nitrans</td>
<td>N amount reallocated from foliage</td>
<td>g N m$^{-2}$</td>
</tr>
<tr>
<td>Nup</td>
<td>actual total N uptake by fine roots</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>Nupcap</td>
<td>intrinsic capacity of the fine roots to absorb soil N</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>Nup2 week</td>
<td>2-week averaged N uptake from the lth layer</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>Nupmax</td>
<td>maximum rate of mineral N absorption</td>
<td>g N g$^{-1}$ FR d$^{-1}$</td>
</tr>
<tr>
<td>Nuppot</td>
<td>potential rate of N uptake from the lth layer</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>ORC</td>
<td>C content of any plant organ</td>
<td>g C m$^{-2}$</td>
</tr>
<tr>
<td>ORCnet</td>
<td>C/N ratio of any given organ</td>
<td>dimensionless</td>
</tr>
<tr>
<td>ORN</td>
<td>N demand by tree organs</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>ORNmax</td>
<td>organ metabolising rate of reserve N into organ N</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>ORNopi</td>
<td>optimum C/N ratio of any given organ</td>
<td>dimensionless</td>
</tr>
<tr>
<td>RESN</td>
<td>N reserve</td>
<td>g N m$^{-2}$</td>
</tr>
<tr>
<td>RESNmax</td>
<td>maximum value of the N reserve</td>
<td>g N m$^{-2}$</td>
</tr>
<tr>
<td>RESNstrs</td>
<td>plant N stress</td>
<td>dimensionless</td>
</tr>
<tr>
<td>RLD</td>
<td>root length density per unit soil volume</td>
<td>cm cm$^{-3}$</td>
</tr>
<tr>
<td>rr</td>
<td>radius of fine roots</td>
<td>cm</td>
</tr>
<tr>
<td>SOILNi</td>
<td>total amount of soil mineral nitrogen</td>
<td>g C m$^{-2}$</td>
</tr>
<tr>
<td>stept</td>
<td>length of the integration time step</td>
<td>d</td>
</tr>
<tr>
<td>SI</td>
<td>amount of sucrose available to growth</td>
<td>g C m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>TRN</td>
<td>tree N content</td>
<td>g N m$^{-2}$</td>
</tr>
<tr>
<td>TRNnet</td>
<td>tree N demand</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>TRNmax</td>
<td>tree metabolising rate of reserve N into organ N</td>
<td>g N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>THKi</td>
<td>thickness of the lth soil layer</td>
<td>m</td>
</tr>
<tr>
<td>Wap_l</td>
<td>plant water uptake in the lth soil layer</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>θ_l</td>
<td>soil water content in the lth soil layer</td>
<td>m$^3$ m$^{-3}$</td>
</tr>
</tbody>
</table>
Table 2 List of model coefficient values and sources

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Units</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atmospheric N deposition under present conditions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NH4⁺</td>
<td>2.1</td>
<td>g N m⁻² y⁻¹</td>
<td>Weissen et al. (1990)</td>
</tr>
<tr>
<td>NO₃⁻</td>
<td>0.7</td>
<td>g N m⁻² y⁻¹</td>
<td>Weissen et al. (1990)</td>
</tr>
<tr>
<td>Average radius of fine roots (rₚ)</td>
<td>0.025</td>
<td>cm</td>
<td>Eisenstat et al. (2000)</td>
</tr>
<tr>
<td>Biological N fixation for temperate deciduous forests</td>
<td>0.7</td>
<td>g N m⁻² y⁻¹</td>
<td>Perry (1994)</td>
</tr>
<tr>
<td>Coarse root turnover rate</td>
<td>0.02</td>
<td>y⁻¹</td>
<td></td>
</tr>
<tr>
<td>Fine root allocation coefficient (γ)</td>
<td>0.075</td>
<td>g⁻¹ N m²</td>
<td>calibrated for this study</td>
</tr>
<tr>
<td>Fine root C density (FRCdens)</td>
<td>0.075</td>
<td>g C cm⁻³ FR</td>
<td>Eisenstat et al. (2000)</td>
</tr>
<tr>
<td>Fine root N retranslocation</td>
<td>0.23</td>
<td>dimensionless</td>
<td>Ferrier &amp; Alexander (1991)</td>
</tr>
<tr>
<td>Leaf N retranslocation for deciduous trees (transN)</td>
<td>0.60</td>
<td>dimensionless</td>
<td>Oja &amp; Arp (1997b)</td>
</tr>
<tr>
<td>Maximum rate of mineral N absorption (Napmax)</td>
<td>0.002</td>
<td>g N g⁻¹ FR d⁻¹</td>
<td>Robinson &amp; Rorison (1983)</td>
</tr>
<tr>
<td>Minimum soil N concentration for root absorption (Nmin)</td>
<td>0.44</td>
<td>g N m⁻³</td>
<td>Gégo (1993)</td>
</tr>
<tr>
<td>Minimum pH for nitrification in forest soils</td>
<td>3.4</td>
<td>dimensionless</td>
<td>Pennington &amp; Ellis (1993)</td>
</tr>
<tr>
<td>NH₄⁺ diffusion coefficient in free solution</td>
<td>10⁻⁵</td>
<td>cm² s⁻¹</td>
<td>Robinson &amp; Rorison (1983)</td>
</tr>
<tr>
<td>NH₄⁺ and NO₃⁻ concentration in soil solution at the root surface</td>
<td>2 × 10⁻⁸</td>
<td>mol cm⁻³</td>
<td>Burns (1980)</td>
</tr>
<tr>
<td>Optimum pH for nitrification in forest soils</td>
<td>6.2</td>
<td>dimensionless</td>
<td>Paavolainen &amp; Smolander (1998)</td>
</tr>
<tr>
<td>Ratio between maximum N reserve and non-reserve tree N</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trees 11 years of age and older</td>
<td>0.25</td>
<td>dimensionless</td>
<td>Piatek &amp; Allen (2000)</td>
</tr>
</tbody>
</table>

leaf fall (Ntrans). Therefore, the mobilisation rate of the available N reserve (MOBNav) is computed as:

\[ MOBNav = \frac{RESN_s}{N/\text{slept}} \quad \text{phase} = 1 \]  (2)

\[ MOBNav = (\text{RESN} - \text{Ntrans})/\text{slept} \quad \text{phase} > 1 \]  (3)

Finally, metabolising rate of reserve N into organ N for the whole tree (TRNmet) is limited to the minimum value of either TRNdem or MOBNav:

\[ TRNmet = \min(\text{TRNdem}, \text{MOBNav}) \]  (4)

and metabolising of reserve N into organ N for specific organs (ORNmet) becomes

\[ ORNmet = TRNmet \times (\text{ORNdem}/\text{TRNdem}) \]  (5)

which implies that ORNmet is equal to ORNdem when the N reserve is large enough so that the N demand is fully met.

Nitrogen uptake

Nitrogen uptake by fine roots is computed separately for NO₃⁻ and NH₄⁺ by solving the steady-state diffusion transport equation for both ions, according to the model of Robinson & Rorison (1983):

\[ C_l = C_{la} - \left( \frac{DF}{4 \pi D b} \right) \times \left( 1 + \frac{\ln(\pi \times r_f^2 \times \text{RLD})}{\ln(\pi \times r_f^2 \times \text{RLD})} \right) \]  (6)

where \( C_l \) is the solute concentration in the bulk soil, and \( DF \) is the solute inflow rate per unit root length (see Table 1 for all variables). The specific \( D \) values for NO₃⁻ and NH₄⁺ are computed according to the equations of Clarke & Barley (1968):

\[ D_{\text{NO}_3} = (0.36 + 22.0 \times \theta) \times 10^{-6} \]  (7)

\[ D_{\text{NH}_4} = (0.98 + 11.06 \times \theta) \times 10^{-7} \]  (8)

The specific \( b \) values for NO₃⁻ and NH₄⁺ are computed according to the equations of Baldwin (1975):

\[ b_{\text{NO}_3} = \theta \]  (9)

\[ b_{\text{NH}_4} = \frac{Dl \times \theta^2}{D} \]  (10)

where \( Dl \) is the solute diffusion in free solution. The value of RLD in each soil layer is computed as

\[ \text{RLD}_i = \frac{FRC_i}{FRCdens \times \pi \times r_f^2 \times CRthk_i \times 10^6} \]  (11)

where \( FRCdens \) is the fine root length density, \( CRthk_i \) is the thickness of a any given soil layer \( l \) colonised by roots, and \( 10^6 \) is a unit conversion factor.

Mass flow transport of NO₃⁻ and NH₄⁺ (MF) is the second process which contributes to fine root N absorption (Robinson & Rorison 1983). In ASPECTS, it is computed as
\[ \text{MFNO}_i = \frac{W_{upi} \times \text{NO}_3}{THK_i \times b_{\text{NO}_3} \times 10^6} \] (12)

\[ \text{MFNH}_4 = \frac{W_{upi} \times \text{NH}_4}{THK_i \times b_{\text{NH}_4} \times 10^3} \] (13)

where \( W_{upi} \) is the plant water uptake in the \( i \)th soil layer as computed in the transpiration and root absorption routines, and \( THK_i \) is layer thickness. Following conversion of MF and DF in the same units, the total potential inflow \((I)_i\) of \( \text{NO}_3^- \) and \( \text{NH}_4^+ \) into the fine root system becomes

\[ I_i = DF_i + MF_i \] (14)

Once the equation is solved and \( I_i \) is determined, it is compared to a maximum physiological capacity for fine root absorption of \( \text{NO}_3^- \) and \( \text{NH}_4^+ \) computed as the minimum value of three separate factors: (1) the plant physiological capacity for N storage, (2) the physiological capacity of the fine roots to absorb N, and (3) the maximum rate of N transfer from the soil to the fine roots. In each soil layer, the intrinsic capacity of the fine roots to absorb soil N \((N_{\text{upi}})\) is computed as the product between the maximum rate of mineral N absorption (see Table 2) and the amount of fine root present in the soil layer. For deciduous trees, \( N_{\text{upi}} \) is set to 0 during the leaf-less winter period. During the growing season, \( N_{\text{upi}} \) is compared to the maximum supply of soil N in each soil layer \((N_{\text{supi}})\) at each time step, which is computed as

\[ N_{\text{supi}} = (\text{SOILN}_i - \text{(N_{min} \times THK}_i)) \times CRat_i/slept \] (15)

where \( \text{SOILN}_i \) is the total amount of soil mineral N, i.e. \( \text{NO}_3^-\text{N} + \text{NH}_4^-\text{N} \), in the \( i \)th soil layer, \( \text{N_{min}} \) is the minimum soil N concentration for absorption by roots, and \( CRat_i \) is the proportion of the \( i \)th soil layer which is accessible to fine roots. For the soil layer where the root front is located \( CRat_i \) is equal to the ratio between the vertical extension of fine roots in the layer and the thickness of the layer, for all upper layers \( CRat_i = 1.0 \). The potential rate of N uptake by fine roots in each soil layer \((N_{\text{upi}})\) is computed as

\[ N_{\text{upi}} = \min(N_{\text{upi}}; N_{\text{supi}}) \] (16)

Fine roots absorb soil N as long as the N concentration in the leaves has not reached their optimum concentration

\[ N_{\text{up}} = \sum_{i=1}^{\text{layers}} N_{\text{upi}}, \quad \text{FRCN} \geq \text{FRCNap} \] (17)

\[ N_{\text{up}} = 0.0, \quad \text{FRCN} < \text{FRCNap} \] (18)

where \( N_{\text{up}} \) is the actual N uptake by fine roots. Certain models compute the N uptake as the minimum value between organ demand and soil supply (Godwin & Jones 1991; Oja & Arp 1997a). Nevertheless, this formulation is not appropriate for models such as ASPECTS that allocate assimilates at sub-daily time steps. Nitrogen consumption by organ growth, especially above-ground, is not instantaneously matched by an equivalent absorption of N by fine roots. In ASPECTS, N demand and root absorption are somewhat dissociated through the use of the N reserve.

\textbf{N litter production and retranslocation}

Plant N is returned to soil litter pools by two distinct mechanisms: (1) harvest, and (2) plant tissue senescence. Nitrogen contained in leaves and fine roots feeds non-woody litter pools, while branch, stem and coarse root N goes into woody litter pools. Nitrogen contained in dead above-ground organs is returned to the litter pool of the uppermost soil layer. Root litter N is returned to the corresponding soil layer. When harvest is simulated, all the N contained in the removed tree organs is returned to soil litter pools, except for stem N which is exported from the forest plot together with stem C.

Retranslocation of N from naturally senescing non-woody organs is simulated by ASPECTS. Literature information suggests that N retranslocation averages 23% for fine roots (Ferrier & Alexander 1991), and 60% for leaves of deciduous trees (Oja & Arp 1997b). The retranslocated N feeds back into the N reserve. A fixed percentage of N retranslocation from senescing organs to the N reserve implies that \( \text{RESN} \) can become temporarily larger than \( \text{RESN}_{\text{max}} \), which prevents N absorption by fine roots.

\textbf{Other elements of the N cycle}

Nitrogen mineralisation from litter pools is computed as a function of litter-C mineralisation rates and the C/N ratio of the litter, as suggested by Johnsson et al. (1987). \( \text{NH}_4^+ \) is the first form of N produced by the mineralisation of the litter and the soil organic matter. This \( \text{NH}_4^+ \) is later transformed into \( \text{NO}_3^- \) at a rate that depends on the soil environmental conditions (Carnol 1999). The ASPECTS nitrification subroutine is based on a modified version of the CERES-Maize algorithms (Jones et al. 1986). The dependence of nitrification on soil water contents was modelled as in CERES-Maize (Jones et al. 1986). Temperature dependence of nitrification in forest soils is still much debated (Carnol 1999). In the absence of experimental consensus, temperature dependence of nitrification was assumed similar to that of root growth, which is described in Rasse et al. (2001b). According to numerous field studies, we added a pH-dependence factor, which increases linearly between a minimum and
an optimum pH for nitrification (see Table 2). A nitrification factor is then computed as the minimum value of the water, temperature, and pH factors for nitrification. The final nitrification rate is a function of this nitrification factor multiplied by the total amount of NH$_4^+$ present in the soil layer, as suggested by Jones et al. (1986).

Leaching of NO$_3^-$ and NH$_4^+$ from any given soil layer is conditional to water drainage from that soil layer. The N concentration of both ionic forms in the soil solution is multiplied by the drainage volume out of any given soil layer to obtain the total amount of N leached from that soil layer. Except for the top soil layer, drainage from an overlaying soil layer is computed as an N input to the subjacent soil layer. Concentrations in NO$_3^-$ and NH$_4^+$ in the soil solution are derived from their total content in the soil layer multiplied by their respective solute buffer power in soils, as suggested by Robinson & Rorison (1983).

Denitrification in ASPECTS is computed according to the model of Parton et al. (1996). In short, this model considers that the maximum rate of denitrification, independently of environmental conditions, is substrate limited either by the total amount of NO$_3^-$ or by the amount of available soil carbon. This second parameter is estimated through the rate of soil heterotrophic respiration. The maximum rate of denitrification is subsequently limited by soil water and soil temperature factors. Denitrification rates are maximum at saturation and are reduced by decreasing soil water contents.

Nitrogen stress to photosynthetic capacity

Two types of N stresses to photosynthetic capacity were considered in this study. First, the maximum rate of carboxylation ($V_{c_{\text{max}}}$) is a function of the N content of the foliage, as described by de Pury & Farquhar (1997) and implemented in ASPECTS (Rasse et al. 2001a). This foliage N stress is computed at each time step. Second, canopy LAI is decreased by reduced N availability, as reported in several studies (Fife & Nambiar 1997; Piatek & Allen 2000; Zak et al. 2000). In ASPECTS, N availability for organ growth is represented by the amount of N contained in the N reserve as compared to its maximum capacity. Therefore, N stress to foliage production ($\text{RESN strs}$) is a function of $\text{RESN max}$ divided by $\text{RESN}$. Sensitivity analyses conducted with ASPECTS indicated that photosynthetic capacity was overly sensitive to the simple ratio $\text{RESN max}$ to $\text{RESN}$, and suggested the following expression to be appropriate for computing $\text{RESN strs}$:

$$\text{RESN strs} = \frac{\sqrt{\text{RESN max}}}{\text{RESN}}$$

(19)

Potential foliage production is divided by this stress factor to obtain the actual maximum LAI.

Model structure for fine root growth and turnover

Root biomass at any time step results from the equilibrium between root growth on the one hand, and root death and turnover on the other hand. The root dynamics model relies on two basic principles well grounded in numerous experimental observations: (1) root longevity decreases with increasing N availability (Durieux et al. 1994; Pregitzer et al. 1995; Ryser 1996; Kubiske et al. 1998), and (2) growth of fine root is stimulated by N absorption (Granato & Raper 1989; Samuelson et al. 1991; Pregitzer et al. 1993; Zhang et al. 2000). In ASPECTS, I translated the first principle as

$$L = \text{RESN strs}$$

(20)

where $L$ is the average fine root longevity. In the absence of literature information, it appeared logical to use the same expression of plant N stress, i.e. $\text{RESN strs}$, for both foliage growth and fine root longevity.

The second basic principle of the root model was translated as

$$\text{FRC}_{\text{at}} = \gamma \times \text{SU} \times N_{\text{uptake}}^{2\text{weeks}} \times \text{RESN strs}$$

(21)

where $\text{FRC}_{\text{at}}$ is the allocation of growth assimilates to fine roots located in the 4th soil layer, $N_{\text{uptake}}^{2\text{weeks}}$ is the average N uptake by fine roots for the 2-week period immediately preceding the time step at which allocation is conducted, and $\gamma$ is a calibration coefficient. Equation (21) implies that induction of root production by N uptake influences actual root growth for a 2-week period following uptake. This assumption is supported by the experimental observation that fine roots of trees display large fluctuations in their population on about a 2-week basis (Sword et al. 1996). The SU term in (22) implies that the allocation of assimilates in response to N uptake is not a fixed quantity but rather is proportional to the total amount of available assimilates. The $\text{RESN strs}$ term in (21) implies that proportionally more N is allocated to fine root growth in response to N uptake when the plant experiences an increased N stress. This concept is experimentally supported by the measured increase in the root-to-shoot ratio of trees under increasing N stress (Haynes & Gower 1995; Tingey et al. 1996; Lee et al. 1998; Zak et al. 2000).

Simulation settings and calibration

Although the present study aims at a theoretical analysis of fine root responses to changing environmental conditions, simulations need to be grounded in experimental data under present environmental conditions. I used data from the 1908-planted beech experimental forest of Vielsalm–Belgium (50°17’ N, 6°00’ E). Stem, branch,
Table 3 Simulated vs. measured carbon pools and fluxes for the Vielsalm beech forest, as the result of the calibration runs conducted under present environmental conditions. Average simulated values correspond to the 1997–1998 period when flux measurements were conducted. Effect of climate on the variability of model estimates is provided by standard deviations computed for nine simulation runs ending from 1994 to 2002. NEE is reported as a positive CO₂ flux from the atmosphere to the forest ecosystem.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Simulated Averages</th>
<th>Std deviations</th>
<th>Measured</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total fine root (0–1 mm) biomass</td>
<td>168</td>
<td>10</td>
<td>160*</td>
<td>g C m⁻²</td>
</tr>
<tr>
<td>LAI</td>
<td>3.67</td>
<td>0.07</td>
<td>3.3–3.7†</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>NEE</td>
<td>378</td>
<td>43</td>
<td>430‡</td>
<td>g C m⁻² y⁻¹</td>
</tr>
<tr>
<td>Soil respiration</td>
<td>617</td>
<td>32</td>
<td>800§</td>
<td>g C m⁻² y⁻¹</td>
</tr>
</tbody>
</table>


Realistic simulation of forest responses to environmental changes requires to select an appropriate length for the simulation period. One the one hand, the simulation period must be long enough so that a new equilibrium is reached independently from the initial conditions. On the other hand, the simulation period must be short enough so that the different environmental scenarios do not result in substantially different forest biomass, which would have confounding effects with the environmental scenarios themselves on ecosystem indicators such as NEE and soil respiration. Sensitivity analyses indicated that applying the environmental scenarios on the last 11 years of forest growth was the best trade-off between reaching equilibrium and preserving forest biomass estimates. Results for present conditions are an average of the 1997 and 1998 simulated values, which correspond to the period of measured data.

Atmospheric CO₂ concentrations ranging from 350 to 700 µmol CO₂ mol⁻¹ were tested, which corresponds to the likely increase in atmospheric CO₂ between the 1990s and the end of the 21st century, as calculated by the scenario IS92a with the Bern model (Houghton et al. 1995). Nitrogen deposition rates for the Belgian Ardennes approximate 2.8 g N m⁻² y⁻¹, with a 3:1 ratio of NH₄⁺ to NO₃⁻ (Weissen et al. 1990). I tested the effects of N deposition rates ranging from 0 to 7.0 g N m⁻² y⁻¹. The rate of biological N fixation in forest soils is a parameter difficult to evaluate. I estimated an average value of 0.7 g N m⁻² y⁻¹ from the review information presented by Perry (1994). Results for the CO₂ and N scenarios are presented for the last year of the 1988–1998 simulation period.

**Results**

**Fine root demography under present conditions**

Simulated fine root distribution throughout the soil profile followed a somewhat inverse exponential relationship with depth, with most of the fine roots contained in the uppermost soil layer (Fig. 1). The simulated fine root distribution agreed fairly well with the measured distribution at this forest site (Fig. 1). This result was obtained even though no attempts were made to account for beech-specific fine root growth patterns. Although there exists such species-specific traits to the distribution of fine roots in temperate forests, numerous studies have reported that fine root densities decrease somewhat exponentially with soil depth (Benedau & Auclair 1989; Janssens et al. 1999; Laitat et al. 2000; Matamala & Schlesinger 2000). Consequently, a root growth model based essentially on N absorption was able to simulate the overall distribution of fine roots throughout soil profiles of temperate forests.

Simulated growth of fine roots throughout the growing season displayed a sharp peak in spring time, followed by a fairly constant level for all soil layers (Fig. 2A). Again, these simulation results concur well with a wide body of published experimental research. Maximum fine root growth during spring time was reported for mixed pine-broad leaf forests in Louisiana (Farrish 1991), oak forests in Tennessee (Joslin et al. 2000), and a northern hardwood forest (Hendrick & Pregitzer 1996). The ASPECTS model also predicted that the proportion of
spring flush to total annual root growth is larger for deeper soil layers than for the uppermost soil layer (Fig. 2B). These simulation results are in good agreement with the extensive data set presented by Hendrick & Pregitzer (1996) on fine root dynamics in northern hardwood forests. These authors report that fine root growth from April to mid-May represents about 25% and 40% of total annual fine root growth for the 0–10 and 30–40 cm soil depths, respectively. For the same period of the year, ASPECTS predicts that fine root growth of beech in the Belgian Ardennes is 16% and 40% of total annual fine root growth for the 0–15 and 15–45 cm soil depths, respectively (Fig. 2B).

Changing N deposition rates and atmospheric CO₂ concentrations

Total fine root biomass, as simulated by ASPECTS, increased with increasing N deposition rates and increasing atmospheric CO₂ concentrations (Fig. 3). Under current N deposition rates, ASPECTS predicted that a doubling of the atmospheric CO₂ concentration will increase fine root biomass by 66%. This value is above the 13–57% range of increase reported in beech seedling and sapling studies (Lee et al. 1998). Nevertheless, the magnitude of the CO₂ growth induction of very young stands might differ from that of mature stands. Matamala & Schlesinger (2000) have recently reported a 86% increase in fine root biomass of 16-y-old *Pinus taeda* under elevated CO₂. The predicted increase in fine root biomass in response to elevated CO₂ depends on the N deposition rates, with the lowest increase at 0.0 and 7.0 g N m⁻², and a maximum increase of about 65% reaching a plateau between 1.0 and 5.0 g N m⁻² (Fig. 3).
Simulated fine root biomass increased by about 30% when the N deposition rate increased from 0.0 to 2.0 g N m$^{-2}$ (Fig. 3). Subsequent increases in N deposition rates had less impact on simulated fine root biomass, which reached a plateau in equilibrium with the atmospheric CO$_2$ concentration. At 350 µmol CO$_2$ mol$^{-1}$, N deposition rates higher than 5.0 g N m$^{-2}$ appear to re-increase simulated fine root biomass.

Uppermost soil layer fine root biomass, as simulated by ASPECTS, was consistently increased by increasing CO$_2$ concentrations, while the response to N deposition was non-linear (Fig. 4). Fine root biomass within that soil layer was lowest at 0.0 and 7.0 g N m$^{-2}$, and reached a CO$_2$-dependent maximum value somewhere in between. This prediction resulted in a pronounced interaction between N and CO$_2$ on the distribution of fine roots among soil layers.

Predicted live fine root biomass results from the estimation of (1) the amount of assimilates partitioned to fine roots, and (2) the longevity of these fine roots. The ASPECTS model predicted that increases in both N and CO$_2$ result in larger amounts of assimilates allocated to the fine roots (Fig. 5). The positive effect of CO$_2$ concentration on assimilates allocated to fine roots increased with increasing N deposition rates. The simulated fine root longevity decreased asymptotically with increasing N availability, and increased somewhat linearly with increasing CO$_2$ concentrations (Fig. 6). Again, the model predicted a pronounced interaction of these two factors on fine root longevity. Hence, a doubling of the atmospheric CO$_2$ concentration increased simulated fine root

![Fig. 4 Simulated fine root biomass in the uppermost soil layer (0–15 cm) as a function of the N deposition rate and the atmospheric CO$_2$ concentration.](image1)

![Fig. 5 Simulated amount of assimilates allocated to fine roots as a function of the N deposition rate and the atmospheric CO$_2$ concentration.](image2)

longevity by 35% and 5% at 0.0 and 7.0 g N m⁻², respectively. The simulated fine root longevity was longest at 0.0 g N m⁻², dropped sharply with increasing deposition rates, and reached a plateau at about 3.0–4.0 g N m⁻². The shorter lifespan obtained for the simulated range of environmental conditions was 0.92 y, and was predicted at 7.0 g N m⁻² and 350 μmol CO₂ mol⁻¹. The longest lifespan obtained for the simulated range of environmental conditions was 3.37 y, and was predicted at 0.0 g N m⁻² and 700 μmol CO₂ mol⁻¹. Consequently, ASPECTS simulations suggest that average longevity of beech roots in the Belgian Ardennes ranges approximately from 1 to 3 years depending on N availability.

The simulated allocation ratio between above- and below-ground organs decreased with increasing atmospheric CO₂ concentrations, suggesting that a larger proportion of assimilates are allocated below-ground as forest ecosystems are exposed to elevated CO₂ (Fig. 7). The magnitude of this response was fairly constant throughout the entire range of simulated N deposition rates, and averaged an approximate 20% reduction in allocation ratio from 350 to 700 μmol CO₂ mol⁻¹. Rates of N deposition had little effects on the above- to below-ground allocation ratio. The allocation ratio was nearly constant between 1.0 and 5.0 g N m⁻², and displayed a sharp but small magnitude increase at 0.0 g N m⁻². At rates higher than 5.0 g N m⁻², the predicted allocation ratio displayed slight fluctuations which seemed to coincide with the ecosystem N saturation.

The simulated NEE was more influenced by the N availability in the ecosystem than by the CO₂ concentration (Fig. 8). The simulated NEE increase by a doubling of the atmospheric CO₂ concentration was 4% and 28% at 1.0 and 7.0 g N m⁻², respectively. The shape of the NEE response curve to increased N deposition indicates that the forest ecosystem is reaching N saturation at the highest deposition rates. Predicted NEE saturation response to increasing N deposition rates started at about 4.0 g N m⁻² under 350 μmol CO₂ mol⁻¹, and at about 6.0 g N m⁻² at 700 μmol CO₂ mol⁻¹.

© 2002 Blackwell Science Ltd, Global Change Biology, 8, 486–503
Simulated soil respiration rates increased nearly linearly with increasing N deposition rates, with only a slight tendency towards saturation at the highest N deposition rates (Fig. 9). Increased atmospheric CO₂ concentrations had little effects on the simulated soil respiration rates. Only under high N deposition did the soil respiration increase under elevated CO₂.

Discussion

Fine root demography under present conditions

Modelling fine root growth and turnover in temperate forests as mainly controlled by the N cycle provided a good description of (1) fine root distribution throughout the soil profile, and (2) the temporal dynamics of these fine roots throughout the year within individual soil layers. This modelling study supports the concept that soil mineral N is the most important factor regulating fine root demography, as previously suggested by Pregitzer et al. (1995). Corollary, this result suggests that soil water is not as important as N in regulating root growth and turnover in temperate forests. In the ASPECTS model, soil water influences root growth through N adsorption, i.e. diffusion and mass flow, and through its control on soil strength and aeration stresses, as explained in Rasse et al. (2001b). Nevertheless, the model does not include direct stimulation of either root growth or turnover by soil water availability. The suggested predominant effect of N on root growth argues for integrating nutrient availability effects into water stress studies on root growth, as proposed by Joslin et al. (2000).

The simulation results suggest that highest root populations in the uppermost soil layer, as reported in numerous studies (Benedau & Auclair 1989; Janssens et al. 1999; Matamala & Schlesinger 2000) are induced by the high N inputs from litter fall and atmospheric depositions on the soil surface. The ASPECTS model predicts that the spring-time flush of fine root growth, as reported in numerous studies (Farrish 1991; Hendrick & Pregitzer,...
1996; Joslin et al. 2000) is attributable to the large amount of mineral N available within the soil profile at springtime, which results from organic matter mineralisation and atmospheric deposition inputs outside of the growing season. In this context, specific information regarding the architecture of the coarse root system does not appear crucial for predicting spatial and temporal fine root demography of trees. The depth of the coarse root system which sustains the fine roots might be the only essential architectural parameter for modelling purposes, as suggested by Rasse et al. (2001b).

### Changing N deposition rates and atmospheric CO₂ concentrations

The predicted increase in fine root biomass under increased N availability agrees with recent results from fertiliser trial experiments (Laitat et al. 2000; Pregitzer et al. 2000b; Zak et al. 2000). Opposite to these results, other studies conducted through N-availability gradients suggested that fine root biomass is negatively correlated with N availability (Nadelhoffer et al. 1985; Vogt et al. 1986). Nadelhoffer (2000) hypothesises that tree fine root biomass decreases under increasing N availability as a result of a decrease in fine root longevity. My simulations indicate that the decrease in fine root longevity concomitant with an increase N availability (Fig. 6) is not sufficient to reduce fine root biomass given (1) the substantial increase in the amount of assimilates available to root growth (Fig. 5), and (2) the stimulation of fine root growth by N uptake as supported in numerous studies (Granato & Raper 1989; Samuelson et al. 1991; Pregitzer et al. 1993; Zhang et al. 2000). Therefore, model quantification supports the hypothesis of an increase in fine root biomass concomitant with an increase N availability. Nevertheless, the model also provides two important clues as to why the experimental results are somewhat contradictory. First, the increase in root biomass is predicted to happen mostly at low N availability (Fig. 3). Hence, there is little difference in predicted fine root biomass between 2.0 and 5.0 mol N m⁻² y⁻¹, but a large increase at 5.0 mol N m⁻² y⁻¹.

© 2002 Blackwell Science Ltd, Global Change Biology, 8, 486–503
5.0 g N m$^{-2}$. Second, the predicted distribution of fine root biomass among soil layers is modified by N availability, which potentially decreases fine root biomass in certain soil layers while N availability is increasing (Fig. 4). For example, the top soil layer harbours a predicted 84, 114, and 72 g C m$^{-2}$ of fine roots at N deposition rates of 0.0, 2.0, and 7.0 g N m$^{-2}$, respectively (Fig. 4). At 0.0 g N m$^{-2}$ deposition, the N supplies comes from soil organic matter, fine root and leaf decomposition, and biological N fixation. Therefore, a fair amount of this N is first made available throughout the soil profile. At 2.0 g N m$^{-2}$ deposition, a substantial amount of mineral N is brought in the forest ecosystem directly on the soil surface. Therefore, the model predicts that fine root growth is stimulated in the uppermost soil layer as compared to deeper layers. This can be interpreted as the fact that tree fine roots must develop in the uppermost soil layer, where the N is first made available, to compete with ground-level vegetation and microbes. At 7.0 g N m$^{-2}$ deposition, N is brought into the ecosystem at a rate higher than the absorption capacity of tree fine roots. There is excess N in the system, and N leaching takes place. Therefore, more N becomes available to deeper soil layers, which favours the growth of fine roots in deeper soil layers. Such a mechanism might not only apply to N deposition but also to lateral drainage as an N source. When N-enriched waters drain laterally through soils of any given forest toposequence, N is made available directly to deeper soil layer fine roots of trees located in the lower part of that toposequence. This might result in decreased fine root populations in the upper part of these soil profiles under increased N availability, while the total root population might actually increase. Model simulations advocate for a correct sampling of the entire depth of the root system to accurately evaluate N effects on fine root populations.

The results of this study indicate that fine root biomass and distribution among soil layers in 21st-century temperate-forest soils will be influenced by interactions between N deposition rates and atmospheric CO$_2$ concentrations, which corroborates recent experimental findings (Pregitzer et al. 2000b; Zak et al. 2000). The

Fig. 9 Simulated soil respiration as a function of the N deposition rate and the atmospheric CO$_2$ concentration.
predicted response of fine root biomass to CO₂, ranging between 40% and 65% depending on N deposition rates (Fig. 3), is close to average experimental values obtained for temperate deciduous and evergreen trees (Lee et al. 1998; Tingey et al. 2000). ASPECTS simulations indicate that fine root biomass increases in response to elevated CO₂ under the double effect of (1) an increase in root longevity due to increased N stress (Fig. 6), and (2) larger amounts of assimilates available to the growth of plant tissue due to increased photosynthesis (Fig. 5). This second point corresponds to the concept of Norby & Jackson (2000) that ‘bigger plants have bigger root systems’, but in addition, the model predicts root-specific responses to elevated CO₂ attributable to interactions with the N cycle.

The decrease in fine root longevity together with increasing N deposition rates comes as a direct consequence of model development hypotheses, and therefore cannot be discussed as a true simulation result. Nevertheless, the predicted range of fine root longevity is worth considering. As discussed above, the predicted increase in fine root biomass by increasing N availability is quite consistent with experimental data. This predicted increase in fine root biomass was fairly moderate only because the predicted fine root longevity decreased by a factor 2.5 from 0.0 to 5.0 g N m⁻² (Fig. 6). A constant or reduced fine root biomass due to increasing N deposition rates would have required an even greater reduction of fine root longevity. My model simulations support the hypothesis that fine root longevity in temperate forests can fluctuate from less than one to several years depending on environmental conditions. These values bracket the about two-year average lifespan of forest fine roots compiled from numerous published studies (Gill & Jackson 2000). Two-year is also the average lifespan reported by van Praag et al. (1988) for fine roots (<1.0 mm) of beech trees growing in the Belgian Ardennes. The possibility of having fine roots of a given species varying in age by several years has recently been experimentally determined by Gaudinski et al. (2001). Therefore, the magnitude of the response falls within the range of experimentally measured values.

The longevity response of tree fine roots to elevated CO₂ remains uncertain from the conflicting and non-significant experimental results obtained up to now. My ASPECTS simulations suggest that the lifespan of fine roots is increased by elevated CO₂ in low-N conditions, and remains fairly unaffected by CO₂ in high-N conditions. This result agrees with the theoretical analysis conducted by Eisenstat et al. (2000). Recently, Matamala & Schlesinger (2000) reported a non-significant 46% increase in fine root longevity under elevated CO₂ for 16-year-old Pinus taeda trees, which agrees with results of previous studies on oak-palmetto scrub ecosystems (Day et al. 1996), and Pinus ponderosa (Tingey et al. 1997). Opposite to these results, other studies have reported a decrease in root longevity under elevated CO₂. Nevertheless, the results of these studies might not be applicable to actual forest ecosystems for two reasons. First, interaction with N was not considered. Thomas et al. (1999) report a significant 3-fold decrease in root longevity under elevated CO₂ during the first two years of CO₂ fumigation of Pinus radiata saplings. Nevertheless, the saplings of this study were fertilised at 60 g N m⁻² y⁻¹, which totally prevented N-stress induced increases in fine root longevity under elevated CO₂. Second, and most important, these studies were based on measuring the short-term responses of very young trees (Norby et al. 1992; Thomas et al. 1999). My simulation suggests that equilibrium fine root responses to elevated CO₂ in mature stands takes several years to reach (data not shown). Hence, prior to the increase in atmospheric CO₂, tree growth and the N cycle are in equilibrium. When suddenly exposed to elevated CO₂ conditions, there is an initial positive growth response which over draws from the N reserve. As a consequence, excessive N is initially sequestered in woody tissues and in the foliage. In addition, fine root turnover remains high because there is no apparent N deficit for the first year or two. When the N reserve is depleted, there is a sudden N stress which reduces plant growth. If, as in the model, the fine root turnover is not immediately adjusted, a large amount of fine roots will die during the second growing season because of the lack of assimilates to sustain them. During subsequent growing seasons, the N contained in the large quantity of leaf litter is released by mineralisation, and fine root turn over slows down, which reduces their N demand. The N reserve is progressively replenished, which is followed by a long-term growth enhancement due to the increased atmospheric CO₂ levels. One could argue that model initialisations are by nature unsteady, implying that this predicted early response does not have a physiological reality. Nevertheless, I think that this incipient predicted response to elevated CO₂ is realistic enough to raise questions about the validity of less-than-3-years sapling studies. There is some experimental evidence suggesting that this mechanism actually takes place. Hence, birch (Betula pendula) saplings under elevated CO₂ saw their root biomass increase in year 1, decrease in year 2, and finally increase in year 4, as compared to the non-fumigated control (Lee et al. 1998).

Root system activities have a preponderant influence on the soil respiration, which is an essential component of the ecosystem NEE (Boone et al. 1998). Consequently, it is important to consider the effects of root growth and turnover on these CO₂ fluxes. The simulations suggest that the capacity of the ecosystem to sequester CO₂, i.e. its NEE, will only begin to saturate at N deposition rates as high as
4.0 g N m$^{-2}$ (Fig. 8). This value was obtained with N as the sole nutrient considered in the simulation, as intended for this theoretical analysis. Therefore, the actual forest ecosystem NEE will potentially saturate at much lower N contents, as other nutrients, e.g. phosphorus or magnesium, become limiting. My simulation results are in good agreement with data presented by Platek & Allen (2000) which indicate that under ambient CO$_2$ *Pinus taeda* forests use over 5.0 g N m$^{-2}$ y$^{-1}$ from fertilisers when not limited by phosphorus and micronutrients.

The model predicts that soil respiration will follow a response to N and CO$_2$ fairly similar to that of NEE (Fig. 9). Vose et al. (1995) reported a fourfold increase in respiration rates of soils under *Pinus ponderosa* from non-fertilised ambient-CO$_2$ to fertilised elevated-CO$_2$ treatments. My model predicts a threefold increase in soil respiration from 0 N 350 µmol CO$_2$ mol$^{-1}$ to 70 N 700 µmol CO$_2$ mol$^{-1}$. Casella & Soussana (1997) reported a 35% increase in below-ground respiration of grass swards under elevated CO$_2$. At current N deposition rate, i.e. 2.8 g N m$^{-2}$, my model predicts a 20% increase in soil respiration from 350 to 700 µmol CO$_2$ mol$^{-1}$. Consequently, a model based on N control of fine root growth and turnover predicted a response of NEE and soil respiration rates to N deposition and elevated CO$_2$ in agreement with published experimental data.

**Acknowledgements**

Funding for this research was provided by the Belgian Federal Office for Scientific, Technical and Cultural Affairs through the BELFORS project (contract no. GC/DD/05E) and by the Communauté Française de Belgique – Direction de la Recherche Scientifique – Actions de Recherches Concertées (contract no. ARC 98/03-219).

**References**


