

# Modelling short-term CO<sub>2</sub> fluxes and long-term tree growth in temperate forests with ASPECTS

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## Abstract

The net ecosystem exchange (NEE) of CO<sub>2</sub> between temperate forests and the atmosphere governs both carbon removal from the atmosphere and forest growth. In recent years, many experiments have been conducted to determine temperate forest NEE. These data have been used by forest modellers to better understand the processes that govern CO<sub>2</sub> fluxes, and estimate the evolution of these fluxes under changing environmental conditions. Nevertheless, it is not clear whether models capable of handling short-term processes, which are mostly source-driven, can provide an accurate estimate of long-term forest growth, which is potentially more influenced by sink- and phenology-related processes. To analyse the interactions between short- and long-term processes, we developed the ASPECTS model, which predicts long-term forest growth by integrating, over time, hourly NEE estimates. Validation data consisting of measurements of NEE by eddy-covariance and forest carbon reservoir estimates were obtained from mixed deciduous and evergreen experimental forests located in Belgium. ASPECTS accurately estimated both: (1) the NEE fluxes for several years of data; and (2) the amount of carbon contained in stems, branches, leaves, fine and coarse roots. Our simulations demonstrated that: (1) NEE measurements in Belgian forests are compatible with forest growth over the course of the 20th century; and (2) that forest history and long-term processes need to be considered for accurate simulation of short-term CO<sub>2</sub> fluxes. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* Deciduous; Eddy covariance; Evergreen; Forest growth; NEE

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## 1. Introduction

Accurate estimates of carbon fluxes between forest ecosystems and the atmosphere are crucial to the evaluation of forested land areas as sinks or sources of atmospheric CO<sub>2</sub>. In this context, sev-

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eral research programmes monitor CO<sub>2</sub> fluxes above temperate forest canopies (Aubinet et al., 2000; Baldocchi, 1997; Greco and Baldocchi, 1996; Valentini et al., 1996). In addition, long-term simulations of forest growth are needed to predict the evolution of carbon stored in forest ecosystems in the course of the next century (Grant and Nalder, 2000). Therefore, models calibrated with short-term carbon fluxes measurements must also prove robust at predicting long-term forest growth.

NEE measurements of CO<sub>2</sub>, based on the eddy covariance method, integrate numerous biological and physical processes affecting the carbon cycle (Malhi et al., 1999). These processes have been described in the literature and translated into models of photosynthesis (de Pury and Farquhar, 1997), stomatal regulation for CO<sub>2</sub> diffusion (Leuning, 1995), partitioning and allocation of assimilates (Gower et al., 1996; McMurtrie, 1985), growth and maintenance respirations (Zogg et al., 1996), litter production, decomposition and mineralisation (Berg et al., 1993), and soil organic matter mineralisation (Parton et al., 1992). Hence, assessing forest NEE through simulation models requires correct assemblage of a series of sub-models describing parts of the carbon cycle. Most of these elements have been combined in forest growth models designed to evaluate long-term carbon storage in forest ecosystems and generally operate on a time step of 1 day or longer (Bossel, 1996; Hoffman, 1995; Korol et al., 1991). On the other hand, models aiming at evaluating short-term ecosystem CO<sub>2</sub> exchanges were also developed and validated (Baldocchi, 1997; Sampson and Ceulemans, 2000). We developed the ASPECTS model (Atmosphere–Soil–Plant Exchange of Carbon in Temperate Sylvae) for the purpose of analysing both the short-term evolution of CO<sub>2</sub> fluxes above the forest canopy and the long-term evolution of carbon reservoirs within tree organs. The objective of this research was to analyse, through simulation models the coherence between hourly eddy-covariance NEE measurements and the long-term accumulation of carbon in leaves, branches, stems and roots of deciduous and evergreen trees of temperate forests.

## 2. Model development

### 2.1. General structure of the ASPECTS model

ASPECTS is a mechanistic model built to predict the evolution of carbon reservoirs in temperate forest ecosystems. Carbon reservoirs are: (1) sugar; (2) starch reserve; (3) foliage; (4) branches; (5) stems; (6) coarse roots; (7) fine roots; (8) soil litter; and (9) soil organic matter (SOM). Because the carbon cycle is closely linked to the water cycle, a complete hydrological module was included in ASPECTS. The general structure of the ASPECTS model is presented in Fig. 1. Although a nitrogen cycle was included in ASPECTS, dynamic feedbacks on the carbon cycle were not considered in this study in order to reduce the number of model-fitting parameters. In addition, the Belgian forests analysed in this study receive substantial amounts of nitrogen through atmospheric deposition, and are unlikely to be nitrogen limited (Weissen et al., 1990). Therefore, the nitrogen cycle will not be further detailed in this article.

The evolution of carbon and water reservoirs is computed at each time step by solving all differential equations defined between incoming and outgoing carbon fluxes. All 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, hourly or half-hourly weather data were available depending on the research site. Although the integration time step is short, 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 reservoir. The ASPECTS model differentiates evergreen from deciduous trees on the basis of the annual phenological cycle, as later described in this article. No species-specific parameters were considered within the evergreen group. In this study, beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) were given specific degree-day requirements for the starting time of leaf expansion and senescence phases, all other parameters remaining equal.

ASPECTS computes rates of photosynthesis according to the theoretical model of de Pury and Farquhar (1997), which is a big-leaf model with a separate integration of sunlit- and shaded-leaf photosynthesis. Canopy photosynthetic capacity ( $V_c$ ) results from the integration of the leaf photosynthetic capacity ( $V_l$ ) over the entire canopy:

$$V_c = \int_0^{\text{LAI}} V_l dL \quad (1)$$

In this model,  $V_l$  is a function of the distribution of leaf nitrogen throughout the canopy, so that Eq. (1) becomes:

$$V_c = \chi_n \int_0^{\text{LAI}} (N_1 - N_b) dL$$

$$= \text{LAI} \chi_n (N_o - N_b) (1 - \exp(-k_n)) / k_n \quad (2)$$

where  $\chi_n$  is the ratio of photosynthetic capacity to leaf nitrogen,  $N_o$  is the leaf nitrogen content on top of the canopy,  $N_b$  is the leaf nitrogen not associated with photosynthesis, and  $k_n$  is the coefficient of leaf-nitrogen allocation in the canopy. Our model calibrations indicated that the theoretical distribution of leaf nitrogen which optimised accuracy of ASPECTS outputs was very close to the optimal distribution presented by de Pury and Farquhar (1997). Parameters used in ASPECTS simulations are presented in Table 1.

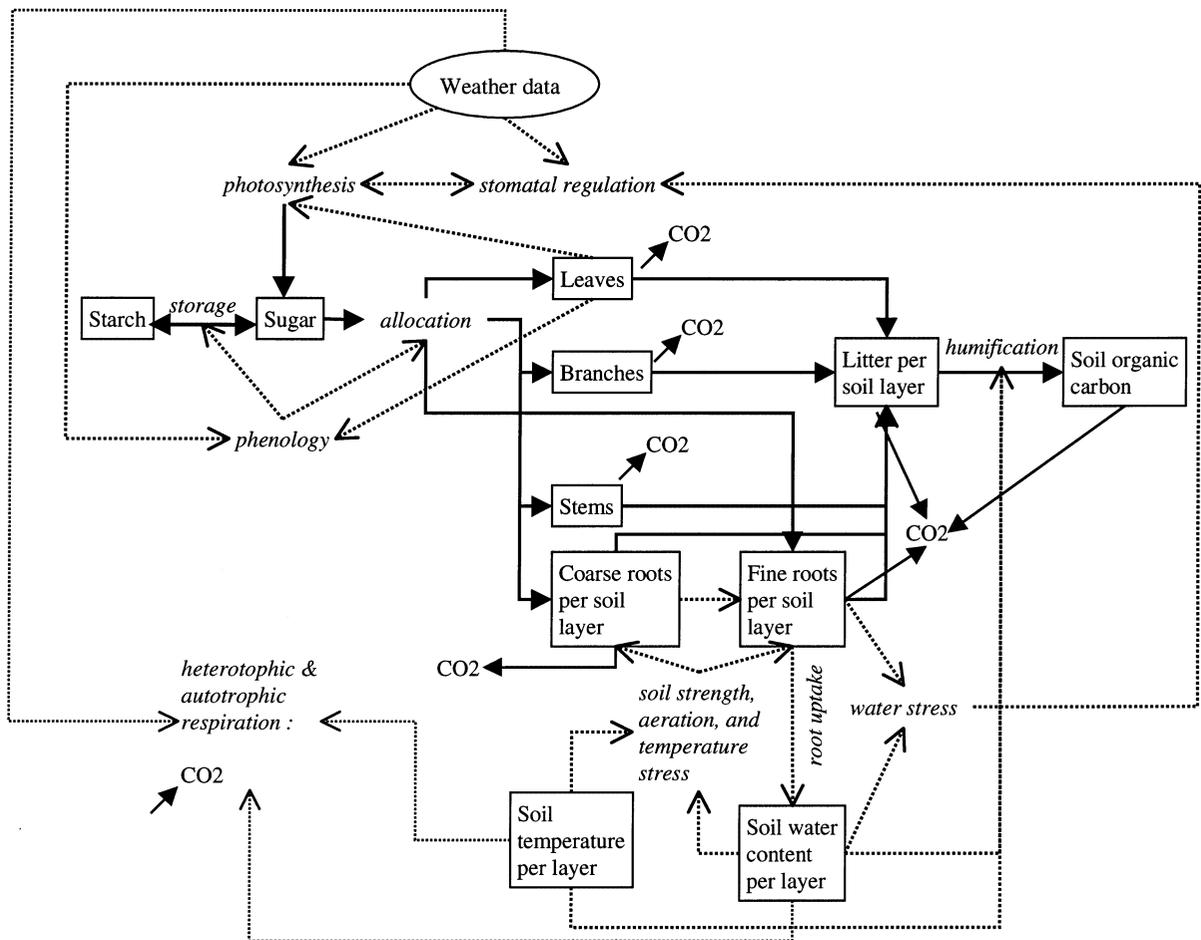


Fig. 1. Diagram of the main carbon-related features of ASPECTS. Solid lines are carbon fluxes, dotted lines are feedback relationships, boxes are carbon, water and temperature pools, and italics represent mechanisms.

Table 1  
List of parameters for ASPECTS simulations

| Model parameters   | Value                 | Units                                  | Source/Notes                |
|--|-----------------------|--|-----------------------------|
| Ratio of photosynthetic capacity to leaf nitrogen ( $\chi_n$ )                       | 0.41                  | mmol mol <sup>-1</sup> s <sup>-1</sup> | calibrated                  |
| Leaf nitrogen not associated with photosynthesis ( $N_b$ )                           | 25                    | mmol m <sup>-2</sup>                   | de Pury and Farquhar (1997) |
| Coefficient of leaf-nitrogen allocation in the canopy ( $k_n$ )                      | 1.78                  |  | calibrated                  |
| Ratio of maximum rates of e <sup>-</sup> transport to carboxylation                  | 2.1                   |  | de Pury and Farquhar (1997) |
| Michaelis-Menten constant of Rubisco for CO <sub>2</sub> ( $K_c$ )                   | 40.4                  | Pa                                     | de Pury and Farquhar (1997) |
| Michaelis-Menten constant of Rubisco for O <sub>2</sub> ( $K_o$ )                    | 24800                 | Pa                                     | de Pury and Farquhar (1997) |
| CO <sub>2</sub> compensation point in the absence of dark respiration ( $\Gamma^*$ ) | 3.69                  | Pa                                     | de Pury and Farquhar (1997) |
| Stomatal conductance ( $g_s$ ) at zero assimilation ( $g_o$ )                        | 0.01                  | mol m <sup>-2</sup> s <sup>-1</sup>    | Leuning (1995)              |
| Coefficient linking $g_s$ to assimilation ( $a_1$ )                                  | 8.5                   |  | calibrated                  |
| Coefficient linking $g_s$ to water vapour pressure deficit ( $D_o$ )                 | 1000                  | Pa                                     | Leuning (1995)              |
| Fraction of respiration to organ growth  | 0.20                  |  | Hoffmann (1995)             |
| Empirical coefficient for maintenance respiration ( $\alpha$ )                       | 2 10 <sup>-4</sup>    |  | calibrated                  |
| Coefficient for C allocation to aboveground organs ( $\delta_{ag-mat}$ )             | 0.43                  |  | calibrated                  |
| Mean residence time of photosynthates in the sugar pool ( $\tau$ )                   | 2.0                   | d <sup>-1</sup>                        | 1/2 of Dewar et al. (1998)  |
| Ratio of fine root to total root C allocation during summer growth                   | 0.75                  |  | Rasse et al. (2001)         |
| Fine root turnover rate  | 1.0                   | year <sup>-1</sup>                     | Hoffmann (1995)             |
| Coarse root turnover rate  | 0.02                  | year <sup>-1</sup>                     | Rasse et al. (2001)         |
| Base temperature for thermal time accumulation for bud burst                         | 5.0                   | °C                                     | Hoffmann (1995)             |
| Coefficient for woody litter decomposition ( $\zeta_w$ )                             | 1.43 10 <sup>-4</sup> | d <sup>-1</sup>                        | calibrated                  |
| Coefficient for non-woody litter decomposition ( $\zeta_{nw}$ )                      | 1.43 10 <sup>-3</sup> | d <sup>-1</sup>                        | calibrated                  |

Within the photosynthesis sub-model, stomatal conductance ( $g_{sc}$ ) is computed by the semi-empirical model of Leuning (1995), as follows:

$$g_{sc} = [g_0 + [(a_1 \times A_n) / ((C_s - \Gamma) \times (1 + D_s/D_0))]] \times F_s \quad (3)$$

where,  $g_0$  is  $g_{sc}$  when the net assimilation ( $A_n$ ) tends towards 0,  $C_s$  is the CO<sub>2</sub> concentration at the leaf surface,  $\Gamma$  is the CO<sub>2</sub> compensation point,  $D_s$  is the water vapor pressure deficit at the leaf surface,  $a_1$  and  $D_0$  are empirical coefficients, and  $F_s$  is factor representing the effect of soil water stress on stomatal regulation. In ASPECTS, values of  $C_s$  and  $D_s$  are considered equal to that of canopy air. Main parameters of the stomatal conductance subroutine are presented in Table 1.

Photosynthetically-fixed carbon is stored in the sugar pool. This pool regulates carbon allocation to plant organs, and is necessary because AS-

PECTS computes photosynthesis at short time steps. Sugar pools, also called sucrose or assimilate pools, have been used in other models that compute photosynthate production at intervals shorter than a day (Dewar et al., 1998; Hoffman, 1995). Sucrose (Su) is allocated to tree organs to satisfy their need for maintenance respiration and growth, which includes both biomass increment and growth respiration. ASPECTS allocates sucrose in priority to maintenance respiration. Organ growth is simulated only when sucrose is available in excess of the energetic demand associated with maintenance respiration. Therefore, sucrose released from the sugar pool at a given rate ( $\tau$ ) is allocated to tree organs according to:

$$Fin_i = \beta \times Rm_i + \delta_i \times AG \quad (4)$$

where,  $Fin_i$  is the influx of carbon to the  $i^{\text{th}}$  reservoir (g C m<sup>-2</sup> d<sup>-1</sup>),  $\beta$  is an allocation coeffi-

cient for maintenance respiration costs,  $Rm_i$  is the maintenance respiration of the  $i$ th carbon reservoir ( $\text{g C m}^{-2} \text{d}^{-1}$ ),  $AG$  is the amount of assimilates available to growth ( $\text{g C m}^{-2} \text{d}^{-1}$ ), and  $\delta_i$  = allocation ratio of  $AG$  for the  $i$ th carbon reservoir (dimensionless). Growth of tree organs at any time step is conditional upon a supply of assimilates from the sugar pool exceeding the energetic demand for maintenance respiration. Therefore, to solve Eq. (4) we need to consider two possible scenarios. First scenario, the total amount of sucrose released from the sugar pool ( $Su/\tau$ ) is smaller than the total maintenance respiration costs ( $\sum Rm_i$ ). In this case, all  $\delta_i$  are set to zero as no sucrose is left available for organ growth. This implies that  $\beta$  becomes:

$$\beta = (Su/\tau) / \sum Rm_i \quad (5)$$

The second scenario happens when  $Su/\tau$  is greater than  $\sum Rm_i$ , which implies that  $\beta$  is equal to 1. The remaining assimilates released from the sugar pool are then partitioned among the different tree reservoirs. In this case,  $AG$  is computed as:

$$AG = (Su/\tau) - \sum Rm_i \quad (6)$$

Growth assimilates are allocated to the different tree organs according to annual phenological phases. For deciduous trees these phases are: (1) winter, no photosynthesis; (2) leaf expansion in the spring; (3) wood production during summer and early fall; (4) leaf senescence. For evergreens, two phases were considered: (1) leaf expansion in the spring, and (2) no leaf growth during the rest of the year. Bud burst is triggered when degree-days accumulated since February 10 over a base temperature of  $5^\circ\text{C}$  reach a thermal time requirement specific to each tree species, following the formula proposed by Hoffman (1995) for beech. Degree-day requirements were computed for beech and oak on the basis of their reported vegetation period (Weissen, 1991). A day length requirement was added to ensure that bud burst was not simulated too early for abnormally warm years. End of leaf growth is simulated when leaf

biomass reaches a maximum value defined by an allometric relationship between maximum leaf biomass and wood biomass, as suggested by Lüdeke et al. (1994). Onset of leaf senescence is simulated when day length becomes shorter than a threshold computed for each species according to published vegetation periods in Belgium (Weissen, 1991). The beginning of the dormancy period is simulated at the end of leaf senescence, when the carbon content of the leaf reservoir reaches zero.

## 2.2. Autotrophic respiration

The ASPECTS model computes maintenance respiration of each tree reservoir prior to allocating assimilates. Measured rates of maintenance respiration for tree leaves, stems, branches and roots display large variability (Ryan et al., 1996). Several published models compute maintenance respiration solely as a function of live tissue biomass and temperature (Hoffman, 1995; Kirschbaum et al., 1994; Running and Gower, 1991; Wang and Jarvis, 1990). However, there is accumulated evidence that maintenance respiration increases proportional to the N concentration of plant tissues (Ryan, 1991; Ryan et al., 1996; Zogg et al., 1996). We generalised the equation proposed by Zogg et al. for fine roots to all tree carbon reservoirs:

$$Rm_i = C_i \times f_{\text{live}} \times \alpha \times N \times \exp(0.1 \times T) \quad (7)$$

where,  $Rm_i$  is the maintenance respiration of the  $i$ th carbon reservoir ( $\text{g m}^{-2} \text{d}^{-1}$ ),  $C_i$  is the total carbon content of the  $i$ th carbon reservoir ( $\text{g m}^{-2} \text{d}^{-1}$ ),  $f_{\text{live}}$  is the fraction of living tissue for the reservoir,  $\alpha$  is an empirical coefficient for maintenance respiration,  $N$  is the nitrogen concentration (% of dry matter), and  $T$  is the temperature of plant tissue ( $^\circ\text{C}$ ). The value of  $f_{\text{live}}$  is 1.0 for the leaves and fine roots, and is equal to the fraction of sapwood for branches, stems and coarse roots. For these woody organs,  $f_{\text{live}}$  is computed according to:

$$f_{\text{live}} = 8.0 \times C_i^{-0.375}, \quad C_i \geq 256 \text{ g Cm}^{-2} \quad (8)$$

$$f_{\text{live}} = 1.0, C_i \leq 256 \text{ g Cm}^{-2}$$

For the same species, identical  $\alpha$  coefficients were taken for leaves, stems, branches and coarse roots. The  $\alpha$  coefficient for fine roots was chosen as three times that of foliage. This ratio was based on observations reported by Ryan (1991) and Ryan et al. (1996). Determination of the  $\alpha$  coefficient is described in the calibration section of this study. Although it has been suggested that respiratory parameters might be species specific (Lavigne and Ryan, 1997) we opted for a single value of  $\alpha$  across species to reduce model tuning parameters in the absence of measured data. The exponential relationship between  $R_m$  and  $T$  in Eq. (7):  $R_m = \text{fct}(e^{0.1 \times T})$  corresponds to an Arrhenius type equation with a Q10 of 2.72. Several reviews of respiration studies have reported that Q10 approximates 2.5 (Raich and Schlesinger, 1992), varies between 1.5 and 3.0 (Ryan, 1991) or between 1.1 and 2.9 (Atkin et al., 2000). Recently, Boone et al. (1998), reported a Q10 of 4.6 for root respiration. Therefore the value of Q10 chosen for this model lies within the range of reported values. Recent studies have suggested that maintenance respiration will not follow a simple Q10 relationship with temperature in the course of the next century because physiological processes will progressively acclimate to the rising temperature, resulting in a lesser than expected increase in respiration rates (Atkin et al., 2000; Gifford, 1995; Tjoelker et al., 1999). As the present study does not deal with future climatic scenarios we have not, as yet, integrated acclimation in the ASPECTS model. Nevertheless, process-based models urgently need mechanistic descriptions of acclimation processes to more accurately predict carbon fluxes in late 21st-century forest ecosystems.

Growth respiration is computed as 20% of AG allocated to each reservoir, as suggested by Hoffman (1995). In addition, growth respiration of fine roots is increased proportional to soil water and temperature stresses (Rasse et al., 2001). This increase in growth respiration represents the additional energetic costs associated with fine root growth in stress conditions.

### 2.3. Assimilate allocation

The ASPECTS model partitions AG between above- and below-ground organs according to phase-dependent ratios. During the leaf expansion phase, all assimilates are allocated to non-woody tissues, i.e., leaves and fines roots, as suggested by Lüdeke et al. (1994). During the wood production phase, ASPECTS simulates allocation as a function of stand age. Hence, studies report that the root to shoot ratio of temperate trees decreases asymptotically with time from saplings to young trees, reaching a minimum value for mature stands (Lee et al., 1998; Vanninen et al., 1996). We developed the following generic relationship for the partitioning of AG to above- and below-ground plant organs as a function of stand age:

$$\delta_{\text{ag}} = \delta_{\text{ag-mat}} \times (1 - \exp(-(2 + \text{age})/5)) \quad (9)$$

$$\delta_{\text{bg}} = 1.0 - \delta_{\text{ag}} - \delta_{\text{starch}} \quad (10)$$

where,  $\delta_{\text{ag}}$  is the fraction of AG allocated to above-ground organs (dimensionless),  $\delta_{\text{ag-mat}}$  is the value of  $\delta_{\text{ag}}$  for unstressed mature trees (dimensionless),  $\delta_{\text{bg}}$  is the fraction of AG allocated to below-ground organs (dimensionless),  $\delta_{\text{starch}}$  is the fraction of AG allocated to the starch reserve (dimensionless), and age is the stand age (years). Growth assimilates allocated to above-ground organs are then partitioned among leaves, branches and stems, while below-ground assimilates are partitioned between coarse and fine roots. The summer wood production and leaf senescence phases have an identical pattern of carbon partitioning among the different tree reservoirs. During these two phases, no assimilates are allocated to leaf growth and 10% of AG is allocated to a starch reserve. The starch reserve is necessary to restart leaf growth of deciduous trees in the spring, so that leaves can start expanding and new assimilates can be allocated to the sugar pool.

### 2.4. Litter production and removal of wood products

Long-term simulations of tree carbon pools require a correct estimation of rates of litter production and removal of wood products. Carbon

stored as foliage of deciduous trees is transferred to the litter pool during the leaf senescence period. Needle senescence from evergreen trees is simulated at a constant rate throughout the year. Tree harvest is simulated by decreasing all tree carbon pools by the amounts of carbon exported from the forest. The assumption is made that harvested stems are removed from the forest, leaving no stem carbon to litter pools. Carbon contained in branches, leaves, fine roots and coarse roots of harvested trees is allocated to the litter pool. Years of harvest and percentages of trees removed are defined in a management file.

Turnover time of fine roots is a crucial parameter that drives the largest carbon input to the soil organic matter. Published data for evergreen and deciduous trees indicate that the duration of fine root turnover cycles approximates 10–12 months (Harris et al., 1977; Usman et al., 1997). Because the life span of fine roots is difficult to estimate precisely, we opted for a value of 1 year, i.e., 365 days.

Litter decomposition is calculated as a simple function of soil water content, temperature, and pH:

$$Ld = C_{Lit} \times 1.83^{(T/10)} \times \zeta \times pH_{fac} \times W_{fac} \times AIR_{fac} \quad (11)$$

where,  $Ld$  is the litter decomposition rate ( $g C m^{-2} d^{-1}$ ),  $C_{Lit}$  is the carbon content of the given litter reservoir ( $g C m^{-2}$ ),  $T$  is the soil temperature ( $^{\circ}C$ ),  $\zeta$  is a coefficient specific to the type of litter ( $d^{-1}$ ),  $pH_{fac}$ ,  $W_{fac}$ , and  $AIR_{fac}$  are dimensionless factors representing the effects of pH, drought and anaerobiosis on litter decomposition. These factors are computed in a similar way as presented in the following section. Litter decomposition is optimal at field capacity and decreases both at low and at high soil water content due to the lack of available water and anaerobiosis, respectively. Temperature dependence of litter decomposition is described in ASPECTS according to the equation of Nemry et al. (1996).

For the purpose of this study, we assumed that soil organic matter (SOM) contents were at equilibrium for periods longer than one year. Annual carbon inputs from litter humification were equated to carbon outputs from SOM mineralisa-

tion. This assumption was guided by two considerations. First, we wanted to restrict the number of parameters affecting annual NEE simulation. Secondly, data of SOM dynamics were not available at the research sites. Therefore, stable SOM content over periods greater than 1 year was the best assumption in the absence of field data.

## 2.5. Water cycle and soil temperature

The main emphasis on modelling hydrology in ASPECTS was for its interaction with the carbon cycle. Below-ground carbon dynamics are influenced by soil strength stress and soil aeration stress, which are related to soil water content (Fig. 1). Soil strength stress is computed according to the equation of Jones et al. (1991):

$$ST_{stress} = BD_{fact} \times \sin[(\theta - \theta_{wp})/(\theta_{fc} - \theta_{wp})] \quad (12)$$

where  $ST_{stress}$  is the soil strength stress,  $BD_{fact}$  is a bulk density factor,  $\theta$  is the soil water content,  $\theta_{fc}$  is the soil water content at field capacity, and  $\theta_{wp}$  is the soil water content at the wilting point. Soil aeration stress is computed as:

$$AIR_{stress} = 1 - [(\theta_{sat} - \theta)/(\theta_{sat} - \theta_{crit})], \theta > \theta_{crit} \quad (13)$$

$$AIR_{stress} = 0, \theta \leq \theta_{crit}$$

where  $\theta_{sat}$  is the soil water content at saturation, and  $\theta_{crit}$  is the threshold for aeration stress and is a function of soil texture and tree species.

ASPECTS simulates stomatal closure in response to soil water deficit according to the methodology presented by Van Wijk et al. (2000):

$$F_s = 1 - k_4 \exp[k_5(\theta_{fc} - \theta)/(\theta_{fc} - \theta_{wp})] \quad (14)$$

where  $F_s$  is the stomatal regulation factor,  $k_4$  and  $k_5$  are empirical coefficients. This regulation tightly links the water cycle to the carbon cycle given that stomatal conductance also regulates the rate of  $CO_2$  uptake by the leaf.

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 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), where the relative humidity (RH) of the air in the top soil layer is:

$$\text{RH} = \exp[(g \times \psi_0)/(R_v \times T)] \quad (15)$$

where  $g$  is  $9.81 \text{ m s}^{-2}$ ,  $\psi_0$  is water potential of the upper boundary soil layer (m),  $R_v$  is the universal gas constant:  $461.89 \text{ J (kgH}_2\text{O)}^{-1} \text{ K}^{-1}$ , and  $T$  is the temperature of the upper soil layer ( $^{\circ}\text{K}$ ). 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.

The soil temperature is calculated in ASPECTS by solving the heat diffusion equation. The spatial and temporal discretizations are the same as in the hydrological module. The heat conductivity in each soil layer is a function of the water pressure head. The bottom boundary condition is a zero heat flux, while at the surface the temperature is assumed equal to the surface air temperature. In this way, the calculation of the surface energy budget is avoided.

### 3. Experimental data

Simulations with ASPECTS were compared to measurements conducted at three Belgian experimental sites located at: (1) Gontrode ( $50^{\circ}58' \text{ N}$ ,  $3^{\circ}48' \text{ E}$ ) (2) Vielsalm ( $50^{\circ}17' \text{ N}$ ,  $6^{\circ}00' \text{ E}$ ); and (3) Brasschaat ( $51^{\circ}18' \text{ N}$ ,  $4^{\circ}31' \text{ E}$ ). General characteristics of experimental sites are summarised in Table 2. Data from the Gontrode experimental forest were used exclusively for model calibration, therefore this experimental site will not be further detailed. The Vielsalm forest plot, covering  $8000 \text{ m}^2$ , is mostly composed of beech for two thirds of the area and of Douglas fir (*Pseudotsuga menziesii* Mirb.) in the rest of the area. Beeches were planted in 1908. Evergreens present in the beech section of the experimental plot are: Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.) and silver fir (*Abies alba* Mill.). Leaf area index was measured by destructive sampling in 1996 and by determination of light transmission through the canopy in 1997 and 1998. Biomass measurements were conducted in 1998 by harvesting four trees from the forest plot. Leaf, stem, and branch biomass were measured. Circumference and height of all trees were measured in 1998. Published allometric relationships were calibrated with the biomass measurements and applied to the entire tree population of the research plot to derive biomass stocks in leaves, stems and branches, as described by Lefèvre et al. (1999). Coarse and fine root biomass were estimated from auger sampling conducted in 1997.

Table 2  
Experimental site description

|  | Vielsalm         | Brasschaat    | Gontrode            |
|--|------------------|---------------|---------------------|
| Mean annual precipitation (mm)                 | 972              | 767           | 752                 |
| Mean annual temperature ( $^{\circ}\text{C}$ ) | 7.5              | 9.8           | 9.6                 |
| Elevation (m)                                  | 490              | 16            | 11–21               |
| Soil type FAO Class                            | Dystric Cambisol | Haplic Podzol | Dystric Pozoluvisol |
| Soil texture                                   | Silt loam        | Sandy         | Sandy loam          |
| Soil pH ( $\text{H}_2\text{O}$ )               | 4.0              | 3.8–4.1       | 3.7–4.5             |
| Soil depth (m)                                 | 1.25             | 1.00          | >1.50               |

All plant tissues were analysed for total carbon and nitrogen. Detailed materials and methods for biomass, carbon and nitrogen measurements at the Vielsalm site have been published 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. Stocking density of the Scots pines was 1390 trees ha<sup>-1</sup> in 1980, 899 trees ha<sup>-1</sup> in 1987, 743 trees ha<sup>-1</sup> in 1990, 716 trees ha<sup>-1</sup> in 1993, 672 trees ha<sup>-1</sup> in 1994, and 556 trees ha<sup>-1</sup> in 1995 (Cermák et al., 1998; Janssens et al., 1999). In 1995, six representative Scots pines were harvested for destructive measurements in a plot identically managed and adjacent to the experimental plot. Leaf, stemwood and branch biomass and LAI were inferred from allometric relationships developed from destructive measurements (Cermák et al., 1998). Fine and coarse root biomass were estimated from measurements conducted on seven wind-blown trees in 1995. Carbon and nitrogen contents of the plant tissue were determined using the dry combustion technique. Detailed materials and methods for plot management, biomass measurements and carbon analyses have been published in Cermák et al. (1998) and Janssens et al. (1999).

Weather data for model inputs were measured on the top of instrumented towers located at the experimental sites. Towers were 40-m high at Vielsalm and Brasschaat, and 35-m high at Gontrode. Data sets consisted of hourly (Gontrode) or half-hourly (Vielsalm and Brasschaat) measurements of: (1) air temperature; (2) solar radiation; (3) precipitation; (4) relative humidity; (5) wind speed; and (6) atmospheric pressure. Available weather data sets for this study were Gontrode 1997, Vielsalm 1997 and 1998, and Brasschaat 1997 and 1998. At the Vielsalm and Brasschaat sites, the CO<sub>2</sub> fluxes exchanged by the forests were measured continuously using the eddy covariance method. A common methodology for the measurement and data treatment, set up in the frame of the EUROFLUX network, was used (Aubinet et al., 2000). NEE data collected at both sites in 1997 and 1998 were available for this study.

#### 4. Simulation settings and calibration

We calibrated and validated ASPECTS with both C-flux and C-reservoir data. Model estimations of carbon fluxes were validated by conducting short-term simulations, while estimations of carbon reservoirs were validated by conducting long-term simulations. These scenarios differ exclusively by the initial conditions and the duration of simulation, all computations and type of outputs being identical. Short-term simulations were conducted for the duration of the available NEE data, i.e., from 1 to 3 years. Initial conditions for the C-flux simulations were set to the measured carbon reservoirs of the leaves, branches, stems and roots. Measurements of maximum LAI from the experimental sites were used for determining the end of the leaf expansion phase. Measured N contents of leaves, branches, stems and roots were used in the calculation of maintenance respiration costs.

Long-term simulations were started by setting initial conditions of tree carbon reservoirs to 1-year old seedling values. Simulations were conducted by repeating the period of available weather data from the year of planting to the year of biomass measurement, which varied from 68 to 90 years depending on the site. Tree harvests from the forest plots were simulated according to plot management records or to reach the current stand density when records were not available. Relationship between maximum LAI and wood biomass for young trees was calibrated on data presented by Vanninen et al. (1996). Maximum LAI of maturing stands were set to the average of the measured values.

Model calibration was conducted with the Gontrode data set and with the 1997 NEE measurements from Vielsalm. The end result of the calibration runs, which will not be detailed in this article, consisted in the determination of the parameters presented in Table 1. ASPECTS was further applied to the simulation of NEE measurements conducted at Vielsalm in 1998 and at Brasschaat in 1997 and 1998, and to the long-term accumulation of carbon in the forest stands of Vielsalm and Brasschaat.

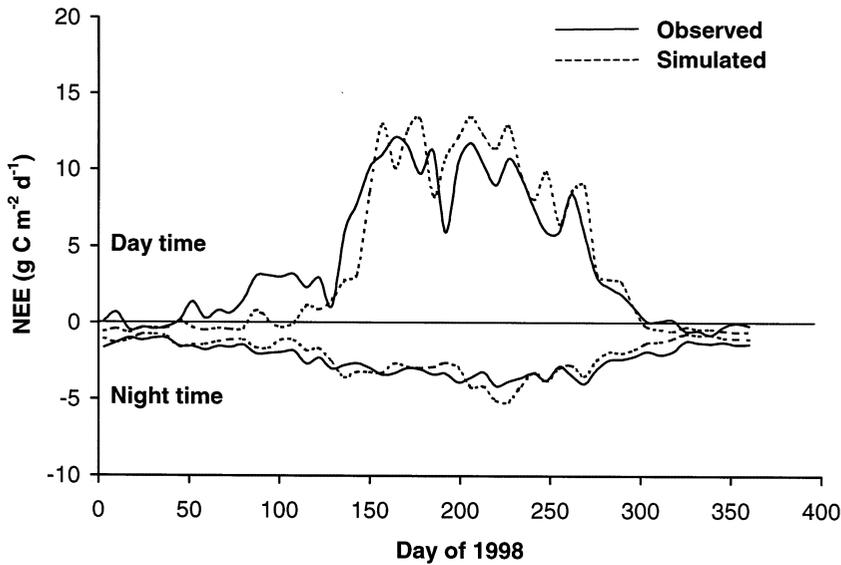


Fig. 2. Simulated vs measured day-time and night-time NEE values for the Vielsalm site in 1998.

The ASPECTS model was designed for simulating carbon fluxes in a single-species forest. Nevertheless, Vielsalm and Brasschaat experimental sites presented a predominant species together with a mix of deciduous and evergreen species. All species present in the ecosystem contribute their respiration and photosynthetic carbon fluxes to the NEE. Therefore, exact species composition must be taken into account for accurate NEE simulations, especially with respect to the ratio of deciduous to evergreen trees. In this study, we ran separate simulations for the different species present in the experimental plots, and calculated weighted averages of the outputs. Proportions of evergreen to deciduous at the experimental sites were difficult to estimate given that these numbers differed substantially whether these ratios were computed on the number of stems, the basal area, or the stem volume. On the basis of plot surveys, we made the approximation that the Vielsalm forest plot is composed of 70% beech trees and 30% evergreen trees, while the Brasschaat forest plot is composed of 70% Scots pine and 30% deciduous trees. All deciduous trees at Brasschaat were simulated as oak.

## 5. Results

### 5.1. Short-term carbon fluxes: NEE

Day-time and night-time NEE values were correctly modelled throughout the year, with RMSE of 1.90 and 0.55  $\text{g C m}^{-2} \text{d}^{-1}$ , respectively (Fig. 2). ASPECTS accurately modelled the daily NEE cycle, although somewhat predicting a lower amplitude of hourly NEE variations (Fig. 3 is an example). The measured data set comprised numerous sharp peaks of  $\text{CO}_2$  emission at night, e.g., on the 6th and 7th of June 1998. These peaks could not be predicted by ASPECTS because the model simulates autotrophic and heterotrophic respiration rates based on processes (i.e., temperature, N content and soil stresses) which do not display such large hourly variations. We suspect that quick variations in the turbulent transport of  $\text{CO}_2$  due to short-term inversions was responsible for these night-time peaks of  $\text{CO}_2$  emission from the forest.

We averaged hourly NEE values for each hour of the day over monthly periods, for each month of the year 1998 (Fig. 4). Overall model predic-

tions were accurate, as simulated values did not significantly differ from measured values for most of the time. Night-time NEE simulations were very close to measured values throughout the year. Autotrophic and heterotrophic respiration are responsible for CO<sub>2</sub> fluxes during night-time (Baldocchi et al., 1997). Therefore, night-time respiration rates were correctly simulated by ASPECTS throughout the year 1998 at Vielsalm. During the daytime, two main significant differences appeared between the measured data and simulated values (Fig. 4). Firstly, the measured daytime NEE were significantly higher than simulated values in March, April and May 98 (Fig. 4). A similar effect was observed to a lesser extent during January, February, November and December 98. Reasons for these differences will be analysed later in the discussion section of this article. Secondly, most simulated NEE values were significantly greater than measured NEE values from 6:00 to 9:00 h from June to September 98, and from 16:00 to 20:00 h from May to September 98. We had observed a similar discrepancy on the calibration runs conducted with the 1997-Vielsalm data set (data not shown). During late afternoons, this discrepancy might result from the fact that the diurnal cycle of canopy air

CO<sub>2</sub> concentration is not simulated by ASPECTS. Hence, canopy air has a tendency to become depleted in CO<sub>2</sub> as the day progresses (Gu et al., 1999), therefore potentially reducing photosynthesis during late afternoons, which was not taken into account by ASPECTS.

ASPECTS was applied to the estimation of the annual NEE at the Brasschaat forest plot in 1997 and 1998 (Fig. 5). The non-interpolated measured data set comprised several periods of missing data. Cumulative measured NEE for the 1997–98 period was  $-118 \text{ g C m}^{-2}$  (Table 3). For the same 2-year period, simulated NEE was  $386 \text{ g C m}^{-2}$ , when simulations were initialised at measured tree carbon reservoirs and conducted for 2 years. Non uniform distribution of missing data throughout the year accounted for part of the difference between measured and simulated NEE. In 1997, simulated NEE peaked during the month of June, while late May and the entire month of June were missing from the data set (Fig. 6). In 1998, a similar pattern of missing data was observed. A month of missing data centred around the first of June contributed to underestimating the annual NEE. Gap filling was conducted by replacing missing data by ASPECTS simulations for the corresponding dates, which yielded a cor-

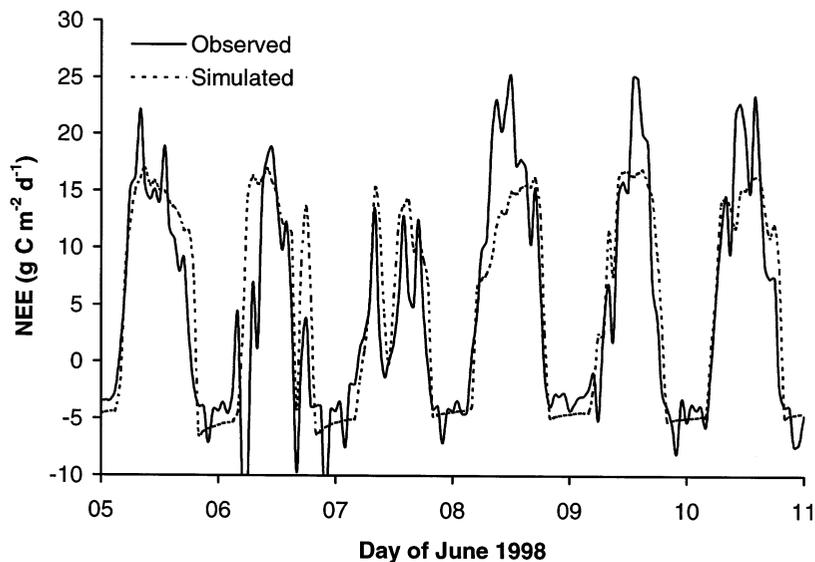


Fig. 3. Comparison between simulated and measured hourly NEE values at Vielsalm from 05 June 98 to 10 June 98.

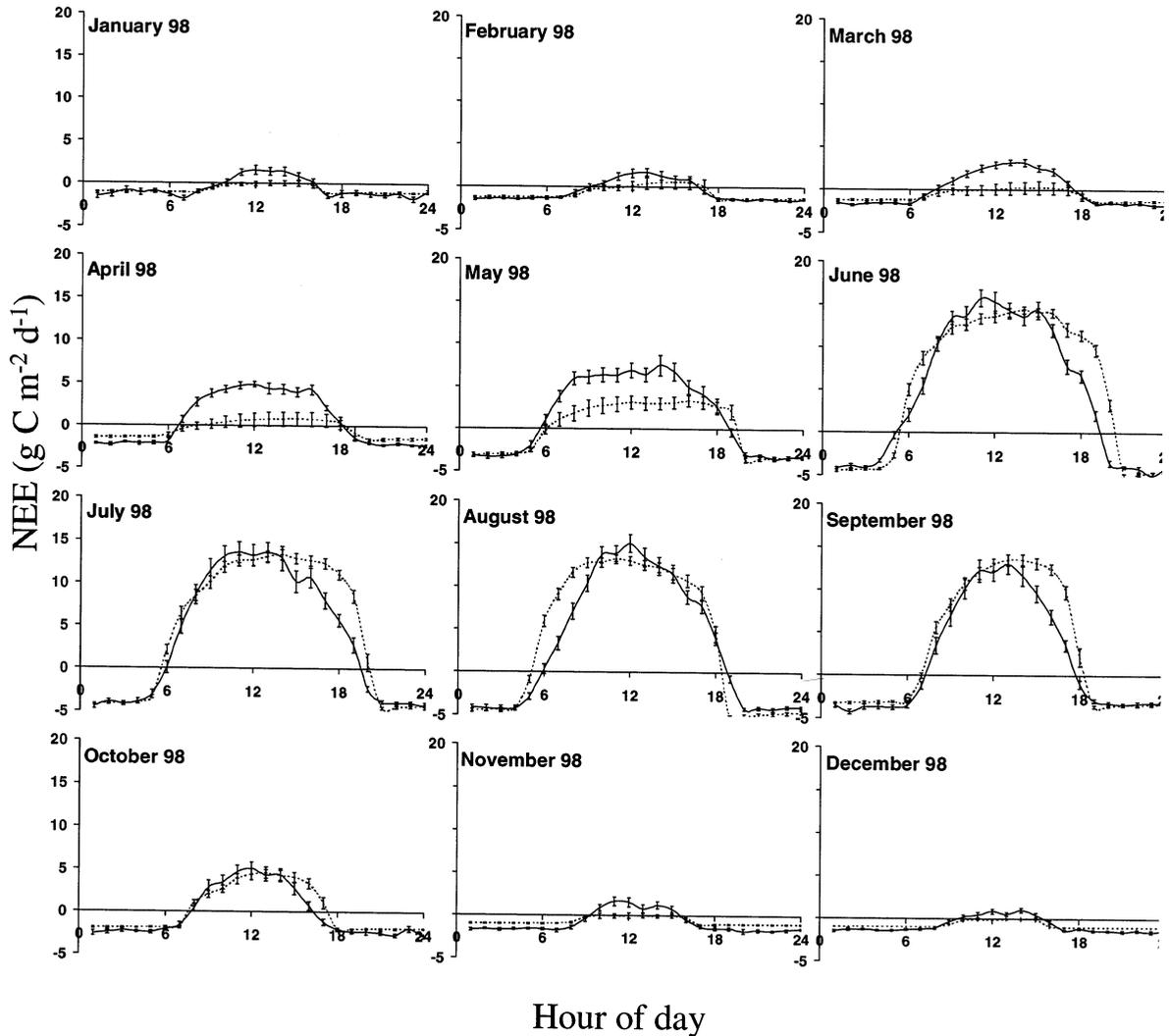


Fig. 4. Comparison for each month of 1998 at Vielsalm between simulated (.....) and measured (—) hourly NEE values averaged for each hour of the day.

rected NEE of  $91 \text{ g C m}^{-2}$  for the 2-year period (Table 3). As expected, the greatest differences between interpolated and non-interpolated data were observed for the 1997 growing season (i.e., from mid-April to mid-October) where peaks of simulated NEE corresponded to periods of missing data.

### 5.2. Long-term carbon fluxes: forest growth

Ninety-year simulations conducted for the Viel-

salm site and 68-year simulations conducted for the Brasschaat site yielded excellent predictions of tree organ carbon contents and ratios (Table 4). Above-ground carbon stored in beech biomass was predicted within 5% of actual measurements. Simulated Scots pine carbon reservoirs for needles, branches, fine roots, and coarse roots were all within 12% of the measured values (Table 4). Simulated stem wood carbon was 19% lower than the measured values. Carbon storage in below-ground organs was simulated within 5% of-

the measured values. All organ ratios, for beech and for Scots pine, were close to the actual measurements (Table 4). Although measured leaf to stem and branch ratios differed substantially between the Vielsalm beeches and the Brasschaat Scots pines, ASPECTS simulations were within 12% of the measured values for both of these ratios.

ASPECTS predicted that biomass accumulation in leaves and needles of Scots pine reached a plateau after 20–25 years (Fig. 6). Total carbon content of woody tissues, i.e. branches, stems and coarse roots, increased until stand age 50 when the multiple harvests conducted in the forest removed woody tissues at a rate higher than the biomass production rate. ASPECTS calculated similar amounts of carbon accumulated in branches and coarse roots, except at an early stand age when carbon accumulation below-ground was favoured. Because of their fast turnover rate, leaves and fine roots were not as affected as woody organs by stand thinning.

Non-woody organs, i.e. leaves and fine roots, generated about three times as much litter than the woody organs, i.e. branches and coarse roots (Fig. 7). We considered that stems were removed from the plots at harvest and therefore did not contribute to woody litter production. Stand thinning had a more pronounced effect on litter production from woody organs than from non woody organs. Total litter production over the life

span of the Brasschaat Scots pine approximated  $27\,000\text{ g C m}^{-2}$ .

## 6. Discussion

ASPECTS produces accurate simulations of both short-term NEE fluxes and long-term forest growth. Our ability to conduct these simulations and the confidence we have in the prediction depend on our knowledge and description of: (1) stand composition; and (2) stand history. An example of model inaccuracy due to insufficient understanding of stand composition is given by the March, April and May daytime NEE simulations at Vielsalm (Figs. 2 and 4). Hence, the results suggest either that the model overestimated spring heterotrophic and/or autotrophic respiration or that it underestimated photosynthesis. This discrepancy is unlikely to result from an overestimation of respiration because a similar effect should have been measured during the night, which was not the case (Fig. 2). Therefore, daytime photosynthesis was underestimated by the model from late-winter to mid-spring. During this period, the beech trees have not yet developed leaves which implies that  $\text{CO}_2$  uptake by the vegetation results exclusively from the photosynthetic activity of the evergreens. Published annual NEE cycles for deciduous temperate forests (Malhi et al., 1999) are in better agreement with

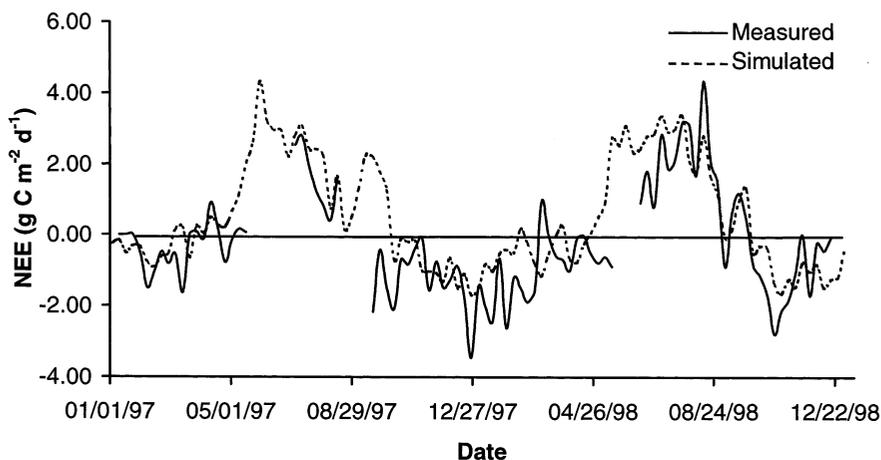


Fig. 5. Comparison between simulated and measured NEE values for the Brasschaat site in 1997 and 1998. Data and values from short-term simulations were averaged on a weekly basis for graphical clarity.

Table 3

Simulated vs measured NEE for the experimental forest of Brasschaat from January 1997 to December 1998

|           | Measured                           |   | Simulated                                       |  |
|-----------|------------------------------------|---|---|--|
|           | Non gap filled $\text{g C m}^{-2}$ | Gap filled <sup>a</sup> $\text{g C m}^{-2}$ | Short-term run <sup>b</sup> $\text{g C m}^{-2}$ | Long-term run <sup>c</sup> $\text{g C m}^{-2}$ |
| 01/01/97  | -66                                | -79   | -28   | -43  |
| -14/04/97 |                                    |   |   |  |
| 15/04/97  | 57                                 | 238   | 327   | 297  |
| -14/10/97 |                                    |   |   |  |
| 15/10/97  | -188                               | -207  | -129  | -169   |
| -14/04/98 |                                    |   |   |  |
| 15/04/98  | 157                                | 239   | 304   | 280  |
| -14/10/98 |                                    |   |   |  |
| 15/10/98  | -77                                | -99   | -88   | -107   |
| -31/12/98 |                                    |   |   |  |
| Total     | -118                               | 91  | 386   | 258  |

<sup>a</sup> Gap filling conducted with short-term simulation runs.

<sup>b</sup> Simulations conducted for two-years using measured tree biomass as initial conditions.

<sup>c</sup> Data represent the last two years of simulated NEE from runs conducted from seedlings to 68-year-old trees.

ASPECTS simulations than with the data obtained for the beech-dominated forest of Vielsalm. In our simulation, a proportion of 30% evergreen was insufficient to correctly simulate the measured NEE fluxes. Therefore, ASPECTS simulations point to a greater than expected influence of evergreens on  $\text{CO}_2$  flux measurements, which might originate from the adjacent Douglas-fir plot. Source regions for eddy flux measurements, which were reported to cover up to 8 ha, depend on wind direction, wind speed, instrument measurement height, and atmospheric stability (Hollinger et al. 1994). Nevertheless, data collected at the Vielsalm site, when the wind was blowing from the direction of the Douglas-fir stand were replaced by interpolated data, which should have reduced lateral influences on measurements. Although we can not exclude that the spring-time discrepancy between measured and simulated values originates from the model, it is also possible that evergreens had a greater than expected influence on NEE measurements at the Vielsalm site.

In addition to stand composition, information regarding stand history is critical to accurately simulating forest carbon reservoirs and fluxes (Fig. 6). At Brasschaat, we were able to accurately predict final biomass for each organ (Table 4)

because the numerous harvests conducted between stand age 50 and 65 were considered in the long-term simulations (Fig. 6). The least accurate simulation was obtained for stem wood carbon of 68-year-old Scots pines, which was underestimated by  $1500 \text{ g C m}^{-2}$  (Table 4). Although this quantity may seem substantial, estimated stem wood carbon removed by harvest from the forest over the same time period was close to  $6000 \text{ g C m}^{-2}$  (data not shown). Therefore, uncertainties as

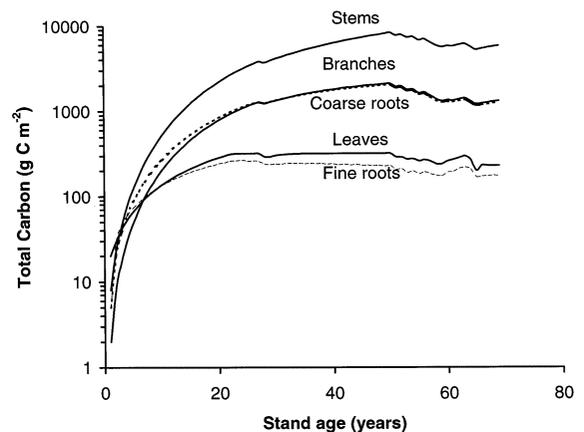


Fig. 6. Simulated evolution of total amounts of carbon contained in leaves, branches, stems, fine roots and coarse roots of the Brasschaat Scots pines.

Table 4

Simulated vs measured carbon reservoirs and organ ratios for 90-year simulation for the beech-dominated forest of Vielsalm, and 68-year simulation for the Scots pine-dominated forest of Brasschaat

|   | Vielsalm |           | Brasschaat |           |
|---|----------|-----------|------------|-----------|
|   | Measured | Simulated | Measured   | Simulated |
| <i>Carbon reservoirs (g C m<sup>-2</sup>)</i> |          |           |            |           |
| Leaves  | 90       | 80        | 300        | 280       |
| Stems   | 7940     | 8000      | 7330       | 5820      |
| Branches                                      | 2530     | 2030      | 1350       | 1305      |
| Fine roots                                    | 340      | 250       | 180        | 164       |
| Coarse roots                                  | 2060     | 1820      | 1280       | 1247      |
| <i>Organ ratios</i>                           |          |           |            |           |
| Above-ground/below-ground                     | 4.4      | 4.8       | 6.2        | 5.2       |
| Leaves/stems & branches                       | 0.0086   | 0.0080    | 0.035      | 0.039     |
| Stems/branches                                | 3.14     | 3.94      | 5.4        | 4.5       |
| Leaves/fine roots                             | 0.26     | 0.31      | 1.7        | 1.7       |
| Branches/coarse roots                         | 1.2      | 1.1       | 1.1        | 1.0       |

to exact forest management history can greatly modify carbon reservoir predictions. In this context, it is interesting to note that measured NEE values suggest that the Brasschaat forest plots are close to equilibrium and therefore no longer substantially fixing carbon (Table 3), while Janssens et al. (1999) reported that annual wood volume increment for the Brasschaat Scots pines was 6–7 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> from 1995 to 1998. For the same 3-year period, ASPECTS simulated a stem wood increment of 150 g C m<sup>-2</sup> year<sup>-1</sup>, which corresponds approximately to 6 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup>. According to the literature, the Scots pine of Brasschaat are in the age group (i.e., from 60 and 90 years old) corresponding to their highest productivity (Weissen, 1991). This apparent contradiction between NEE and stemwood volume increments implies that a strong source of CO<sub>2</sub> compensated for carbon sequestration by the growing Scots pines. Soil respiration represents the largest carbon flux from forest ecosystems to the atmosphere (Law et al., 1999; Malhi et al., 1999). Heterotrophic soil respiration from litter and SOM mineralisation is modified by tree harvest for a period of several years following cutting (Pastor and Post, 1986). Our long-term simulations suggest that between 1980 and 1995, tree harvest generated 2800 g C m<sup>-2</sup> of dead woody tissues from branches and coarse roots (Fig. 7).

This slow-decomposing material remained in the forest plot and contributed to heterotrophic respiratory fluxes for numerous years following harvest. During the same period of time, leaf senescence and fine root turnover generated 5500 g C m<sup>-2</sup> (Fig. 7). Nevertheless, these dead non-woody tissues did not substantially affect long-term heterotrophic respiratory fluxes because of their fast decomposition rate. During the long-term runs, simulated decomposition of the woody litter reduced the predicted NEE for 1997 and 1998 by 127 g C m<sup>-2</sup>, compared to short-term simulations conducted for 2 years and initialised



Fig. 7. Simulated cumulative litter production for the non woody organs (i.e., leaves and fine roots) and for the woody organs (branches and coarse roots) of the Brasschaat Scots pine. Stems litter was not simulated as stems are removed from the plots at harvest.

at measured forest carbon reservoirs (Table 3). Therefore, our simulations support the hypothesis that lower than expected measured NEE is in part attributable to the recent massive removal of trees conducted in the Brasschaat experimental forest.

With the ASPECTS model we obtained for Brasschaat an average annual NEE of 193 and 129 g C m<sup>-2</sup> year<sup>-1</sup> with short-term and long-term simulations, respectively. Because there were large amounts of missing data for this experimental site, the true value of the NEE is unknown. For the same site, Sampson and Ceulemans (2000), using the SECRETS model estimated that the annual NEE ranged between 220 and 390 g C m<sup>-2</sup> year<sup>-1</sup>, while Valentini et al. (2000) estimated this value to be 157 g C m<sup>-2</sup> year<sup>-1</sup>. We think that our value of about 130 g C m<sup>-2</sup> year<sup>-1</sup> is the most accurate because it takes into account the long-term history of the forest, which was not the case for the SECRETS simulations. Therefore, ASPECTS has the potential of improving NEE estimates as compared to other existing models.

The ASPECTS model gave reliable estimates over a wide range of temporal scales, from hourly CO<sub>2</sub> fluxes (Fig. 3) to carbon accumulation in tree biomass over periods of 70–90 years (Table 4). Although ASPECTS was not designed for the sole purpose of simulating hourly and daily CO<sub>2</sub> fluxes, it simulated these fluxes with an accuracy equivalent to that of recent models oriented towards short-term simulations, as observed when comparing our results (Figs. 2–4) to recent simulations reported for *ecosys* (Grant and Nalder, 2000), CANPOND and SPA (Law et al., 2000b), and CANOAK (Baldocchi, 1997). Although ASPECTS slightly underestimated daily NEE peaks (Fig. 2), a similar underestimation was reported for *ecosys* (Grant and Nalder, 2000). In addition, ASPECTS simulated the annual trend of CO<sub>2</sub> fluxes more accurately than models operating with a monthly time step such as 3-PG and PnET-II, as observed when comparing results of Fig. 2 to recent simulation results presented by Law et al., (2000a). The ASPECTS model gave reliable estimates of long-term carbon accumulation in tree biomass (Table 4) without the need for a long-term calibration factor, as the calibration was

conducted on short-term CO<sub>2</sub> fluxes. ASPECTS long-term estimates were of comparable accuracy to those of models designed specifically for predicting long-term growth of temperate trees and calibrated on long-term growth data such as the FAGUS model (Hoffman, 1995).

In conclusion, we have demonstrated that the ASPECTS model produces coherent predictions of short-term NEE fluxes and long-term forest growth. Such a coherence is vital to reliable estimates of forest growth in the course of the next century (Grant and Nalder, 2000). In addition, our simulations suggest that species composition of the forest surrounding the measuring tower and history of site management are two important parameters that need to be considered for proper modelling and extrapolation of NEE data.

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### References

- Atkin, O.K., Edwards, E.J., Loveys, B.R., 2000. Response of root respiration to changes in temperature and its relevance to global warming. *New Phytol.* 147, 141–154.
- Aubinet, M., Grelle, A., Ibrom, A., Rannik, U., Moncrieff, J., Foken, 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., 1997. Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant Cell Environ.* 20, 1108–1122.
- Baldocchi, D.D., Vogel, C.A., Hall, B., 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agric. For. Meteorol.* 83, 147–170.

- Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., Calvo de Anta, R., 1993. Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry* 20, 127–159.
- Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396, 570–572.
- Bossel, H., 1996. TREEDYN3 forest simulation model. *Ecol. Model.* 90, 187–227.
- Cermák, J., Riguzzi, F., 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., 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.
- Dewar, R.C., Medlyn, B.E., McMurtrie, R.E., 1998. A mechanistic analysis of light and carbon use efficiencies. *Plant Cell Environ.* 21, 573–588.
- Gifford, R.M., 1995. Whole plant respiration and photosynthesis of wheat under increased CO<sub>2</sub> concentration and temperature: long-term vs. short-term distinctions for modelling. *Global Change Biol.* 1, 385–396.
- Gower, S.T., Pongracic, S., Landsberg, J.L., 1996. A global trend in below ground carbon allocation: can we use the relationship at smaller scales? *Ecology* 77, 1750–1755.
- Grant, R.F., Nalder, I.A., 2000. Climate change effects on net carbon exchange of a boreal aspen-hazelnut forest: estimates from the ecosystem model *ecosys*. *Global Change Biol.* 6, 183–200.
- Greco, S., Baldocchi, D., 1996. Seasonal variations of CO<sub>2</sub> and water vapour exchange rates over a temperate deciduous forest. *Global Change Biol.* 2, 183–197.
- Gu, L., Shugart, H.H., Fuentes, J.D., Black, T.A., Shewchuk, S.R., 1999. Micrometeorology, biophysical exchanges and NEE decomposition in a two-story boreal forest-development and test of an integrated model. *Agric. For. Meteorol.* 94, 123–148.
- Harris, W.F. Jr., Kinerson, R.S., Edwards, N.T., 1977. Comparison of belowground biomass of natural deciduous forest and loblolly pine plantations. *Pedobiologia* 17, 369–381.
- Hoffman, F., 1995. FAGUS, a model for growth and development of beech. *Ecol. Model.* 83, 327–348.
- Hollinger, D.Y., Kelliher, F.M., Byers, J.N., Hunt, J.E., McSeveny, T.M., Weir, P.L., 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75, 134–150.
- Janssens, I.A., Sampson, D.A., Cermák, J., Meiresonne, L., Riguzzi, F., Overloop, S., 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., Williams, J.R., 1991. Simulation of root growth. In: Hanks, J., Ritchie, J.T. (Eds.), *Modeling Plant and Soil Systems*. Agronomy, 31. American Society of Agronomy, Madison, WI, pp. 91–123.
- Kirschbaum, M.U.F., King, D.A., Comins, H.N., McMurtrie, R.E., Medlyn, B.E., Pongracic, S., 1994. Modelling forest response to increasing CO<sub>2</sub> concentration under nutrient-limited conditions. *Plant Cell Environ.* 17, 1081–1099.
- Korol, R.L., Running, S.W., Milner, K.S., Hunt, E.R. Jr., 1991. Testing a mechanistic carbon balance model against observed tree growth. *Can. J. For. Res.* 21, 1098–1105.
- Laitat, E., Chermanne, B., Portier, B., 1999. Biomass, carbon and nitrogen allocation in open top chambers under ambient and elevated CO<sub>2</sub> and in a mixed forest stand. A tentative approach for scaling up from the experiments of Vielsalm. In: Ceulemans, R., Veroustraete, F., Gond, V., Van Rensbergen, J. (Eds.), *Forest Ecosystem Modelling, Upscaling and Remote Sensing*. SPB Academic Publishing BV, The Hague, The Netherlands, pp. 33–60.
- Lavigne, M.B., Ryan, M.G., 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiol.* 17, 543–551.
- Law, B.E., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biol.* 5, 169–182.
- Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D., 2000a. Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biol.* 6, 155–168.
- Law, B.E., Williams, M., Anthoni, P.M., Baldocchi, D.D., Unsworth, M.H., 2000b. Measuring and modelling seasonal variation of carbon dioxide and water vapour exchange of a *Pinus ponderosa* forest subject to soil water deficit. *Global Change Biol.* 6, 616–630.
- Lee, H.S.J., Overdieck, D., Jarvis, P.G., 1998. Biomass, growth and carbon allocation. In: Jarvis, P.G. (Ed.), *European Forests and Global Change: the likely impacts of rising CO<sub>2</sub> and temperature*. Cambridge University Press, Cambridge, UK, pp. 126–191.
- Lefèvre, F., Laitat, E., Medlyn, B., Aubinet, M., Longdoz, B., 1999. Carbon pools and annual carbon fluxes in the beech forest sub-plot at the Vielsalm pilot station. In: Ceulemans, R., Veroustraete, F., Gond, V., Van Rensbergen, J. (Eds.), *Forest Ecosystem Modelling, Upscaling and Remote Sensing*. SPB Academic Publishing bv., The Hague, The Netherlands, pp. 137–154.
- Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C<sub>3</sub> plants. *Plant Cell Environ.* 18, 339–355.
- Lüdeke, M.K.B., Badeck, F.-W., Otto, R.D., Häger, C., Dönges, S., Kindermann, J., 1994. The Frankfurt biosphere model: a global process-oriented model of seasonal and long-term CO<sub>2</sub> 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., 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., Jarvis, P.G., 1999. The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ.* 22, 715–740.
- McMurtrie, R.E., 1985. Forest productivity in relation to carbon partitioning and nutrient cycling: a mathematical model. In: Cannell, M.G.R., Jackson, J.E. (Eds.), *Attributes of Trees as Crop Plants*. Institute of Terrestrial Ecology, Penicuik, UK, pp. 194–207.
- Nemry, B., François, L., Warnant, P., Robinet, F., Gérard, J.-C., 1996. The seasonality of the CO<sub>2</sub> exchange between the atmosphere and the land biosphere: a study with a global mechanistic vegetation model. *J. Geophys. Res.* 101, 7111–7125.
- Parton, W.J., McKeown, B., Kirchner, V., Ojima, D., 1992. CENTURY users' manual. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, 41 p.
- Pastor, J., Post, W.M., 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2, 3–27.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–89.
- Rasse, D.P., Longdoz, B., Ceulemans, R., 2001. TRAP: a modelling approach to below-ground carbon allocation in temperate forests. *Plant Soil* 229, 281–293.
- Running, S.W., Gower, S.T., 1991. FOREST-BGC, A general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9, 147–160.
- 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., 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.
- Sampson, D.A., Ceulemans, R., 2000. SECRETS: simulated carbon fluxes from a mixed coniferous/deciduous Belgian forest. In: Ceulemans, R.J.M., Veroustraete, F., Gond, V. (Eds.), *Forest Ecosystem Modelling, Upscaling and Remote Sensing*. SPB Academic Publishing, The Hague, The Netherlands, pp. 95–108.
- Saxton, K.E., Rawls, W.J., Romberger, J.S., Papendick, R.I., 1986. Estimating generalized soil-water characteristics from texture. *Soil. Sci. Soc. Am. J.* 50, 1031–1036.
- Tjoelker, M.G., Oleksyn, J., Reich, P.B., 1999. Acclimation of respiration to temperature and CO<sub>2</sub> in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biol.* 5, 679–691.
- Usman, S., Rawat, Y.S., Singh, S.P., Garkoti, S.C., 1997. Fine root biomass production and turnover in evergreen forests of Central Himalaya, India. *Oecologia Montana* 5, 4–8.
- Valentini, R., De Angelis, P., Matteucci, G., Monaco, S., Dore, S., Scarascia Mugnozza, G.E., 1996. Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biol.* 2, 199–207.
- Valentini, R., Matteucci, G., Dolman, A.J., Sculze, E.-D., Rebmann, C., Moors, E.J., 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404, 861–864.
- Van Wijk, M.T., Dekker, S.C., Bouten, W., Bosveld, F.C., Kohsiek, W., Kramer, K., 2000. Modeling daily gas exchange of a Douglas-fir forest: comparison of three stomatal conductance models with and without a soil water stress function. *Tree Physiol.* 20, 115–122.
- Vanninen, P., Ylitalo, H., Sievänen, R., Mäkelä, A., 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). *Trees* 10, 231–238.
- Viterbo, P., Beljaars, C.M., 1995. An improved land surface parametrization scheme in the ECHWF model and its validation. *J. Clim.* 8, 2716–2748.
- Wang, Y.P., Jarvis, P.G., 1990. Description and validation of an array model — MAESTRO. *Agric. For. Meteorol.* 51, 257–280.
- Weissen, F., 1991. Le fichier écologique des essences. Part 2. Ministère de la Région Wallonne. Namur, Belgique. 190 p.
- Weissen, F., Hambuckers, A., Van Praag, H.J., Remacle, J., 1990. *Plant and Soil* 128, 59–66.
- Zogg, G.P., Zak, D.R., Burton, A.J., Pregitzer, K.S., 1996. Fine root respiration in northern hardwood forests in relation to temperature and nitrogen availability. *Tree Physiology* 16, 719–725.