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C allocation among fine roots, above-, and belowground wood in a deciduous forest and its implication to ecosystem C cycling: a modelling analysis

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Abstract

Knowledge about allocation of carbohydrates among tree organs with different life times and decomposition rates is crucial in determining the residence time of carbon (C) in forests and the overall ecosystem C cycling rate. A new model (named CAF) able to simulate C allocation among fine roots, above-, and belowground wood in deciduous forests was developed and integrated into the net ecosystem exchange model FORUG.

CAF draws on growth rules and source-sink relationships. Maintenance and growth of the modelled sinks i.e. fine roots, coarse roots, stems, and branches, are controlled by phenology, environment, and by the reserve of non-structural carbohydrates. CAF was parameterized for 2-y and tested against 6-y observations from a beech (*Fagus sylvatica* L.) stand in North-East France, experiencing summer droughts of different intensities.

The model reproduced well (i) the C fluxes allocated annually to assimilation, respiration and biomass production, and (ii) the interannual pattern of wood biomass accumulation. Seasonality of C reserve and wood growth was captured, but some discrepancies were detected at the onset of the growing season.

The allocation pattern differed among years, although the overall net primary production decreased only in case of severe drought. During a year with severe drought, the fraction of C allocated to production of fast-decomposing C pools (e.g. fine roots, C reserve) increased by +13% than years without drought, whereas the same fraction increased on average by +18% in case of low to moderate drought. Carbon invested in biomass during a year with summer drought has therefore a shorter residence time in the ecosystem than the C stored during a year without summer drought.

1 Introduction

Forest ecosystems store about 1200 10^{15} g carbon (C), equivalent to 52% of the terrestrial C pool (Adams et al. 1990), and are thought to be the largest terrestrial C sink, accumulating about 1 to 3 $10^{15}\,\mathrm{g\,C\,y^{-1}}$ (Malhi et al. 1999). Small changes in the C balance of these ecosystems can therefore have large impact on the atmospheric CO_2 concentration and global climate change. Assimilate allocation among plant processes (e.g. respiration, biomass production) and organs (e.g. leaves, fine roots, branches, stems, coarse roots) is a key process in the C cycle because it determines the residence time of C in the ecosystem. For example, C used to fuel maintenance respiration returns to the atmosphere within few hours-days; C allocated to structural biomass of organs with high turnover and decomposition rate, as fine roots, returns to the atmosphere within few months–years, whereas C allocated to organs with lower turnover and decomposition rate, as stemwood, returns to the atmosphere only after decades or centuries. In other words, allocation crucially determines rates of ecosystem respiration, the major C flux released by ecosystems (Trumbore, 2006). Nonetheless, assimilate allocation is among the processes typically described in lesser detail in C cycle models and rarely tested against datasets at interannual scale.

The development of allocation procedures for C cycle models can rely on strategies used to model C allocation in forest- and single tree growth model. Accordingly, assimilate allocation can be modelled following systems based on: (1) empirical allocation coefficients, (2) growth rules, (3) source-sink relationships, and (4) transport-resistance models. (1) Empirical allocation coefficients define the proportion of assimilates to be allocated to each process or organ. This approach determines a fixed allocation scheme (Lacointe, 2000). (2) Growth rules describe a priori growth patterns and the C fluxes are considered more as a consequence than a determinant of these patterns (Lacointe, 2000). Growth rules comprise (i) architectural rules, (ii) allometric relationships, and (iii) functional balances (i.e. allometric relationships with a functional or adaptive meaning, Lacointe, 2000). Examples of functional balances are the root-shoot ratio and the relationship between sapwood and foliage or Pipe-Model (Cannell and Dewar, 1994; Lacointe, 2000). (3) According to the source-sink relationships-based approach, trees are considered as a collection of semi-autonomous, yet interacting sinks (e.g. fine roots, stems) competing for the supply of assimilates from sources (leaves, reserves) (Le Roux et al., 2001). The amount of C allocated to the sinks depends on specific sink demands. In case available C is not sufficient to satisfy these demands, then every sink is partly satisfied on the same degree, or a sink hierarchy is established, according to which sinks with the highest priority can be fully satisfied and sinks with lower priority receive only the remaining C (Le Roux et al., 2001). (4) The transport-resistance models (TR models; Thornley, 1972a, 1972b; Thornley and Johnson, 1990) simulate C allocation by modelling C transport within the plant and C consumption by the organs (sinks). As reviewed by Lacointe (2000), substrate transport in TR models depends on concentration gradients and flow resistances following the Münch flow theory, whereas sink growth rates are modelled following a bi-substrate kinetic for dry mass growth.

The TR approach is the most mechanistic, whereas the empirical coefficients approach the least (Lacointe, 2000). In fact, TR models simulate the basic translocation mechanism, whereas empirical models focus on the result of the translocation process, the growth pattern of the different plant parts (Lacointe, 2000). Practical application of TR models is however problematic because of their complexity and because model parameters are difficult to estimate (Lacointe, 2000; Le Roux et al., 2001). On the other hand, C allocation module based on growth rules and source-sink relationships are widely used (Lacointe, 2000). This for at least four reasons: (1) although not as mechanistic as the TR models, the formulation of these models comprise a description of the basic mechanisms controlling allocation. (2) Their parameters have in general a clear physiological meaning and can be easily obtained from direct measurements or calibration. (3) They can be coupled to environmental variables and phenology, making them applicable in a wide range of environmental conditions and temporal scales. (4) They are straightforward and easy to develop and use.

A major difficulty in modelling C allocation is the simulation of the growth of leaves, which are concurrently sources, sinks and storage site of C. Furthermore, annual maximal leaf biomass, and its interannual variability, depends on the status of the other tree organs because it is linked to stand structure, previous year growth and current content of C reserve (Le Dantec et al., 2000; Bréda et al., 2006). Consequently, to properly model whole-stand C allocation, two consecutive steps have to be made. First, a sub-allocation module has to be developed for organs other than leaves (branches, stems, coarse roots and fine roots) and tree C reserve (non-structural carbohydrates) (Cannell and Dewar, 1994; Lacointe, 2000; Le Roux et al., 2001). Second, a leaf component has to be integrated to the module taking into account the effects that the other organs have on leaf growth.

In this study, we address the first step of this complex procedure for deciduous forests. We develop a sub-allocation module between aboveground woody compartment (branches, stems), belowground wood (coarse roots), and fine roots based on growth rules and source-sink relationships. Then, we parameterize it for a beech stand and we test it against 6-y datasets of biomass production, standing biomass, C reserve, respiration and phenological observations. Finally, we use the simulations to discuss seasonal and interannual variations of C allocation as affected by naturally occurring variability of environmental conditions, particularly drought stress. Main research questions are therefore: (1) Can a model based on growth rules and source-sink relationships satisfactorily describe C allocation among aboveground woody compartment (branches, stems), belowground wood (coarse roots), and fine roots of a deciduous forest? (2) Are there variations in C allocation among years with different environmental conditions and which implications do they have on C cycling?

2 Materials and methods

2.1 Allocation model CAF

In the new allocation model CAF (Carbon Allocation for FORUG), non-foliar vegetation is divided into four C pools corresponding to the main tree organs i.e. fine roots (W_R), coarse roots or underground wood (W_U), stem wood, (W_S), and branch wood (W_B) plus the assimilate reserve pool (AR), which are stored in each organ. When considered together, coarse roots, stems, and branches, are referred to as “woody pool” or “wood” (W). We simulated C allocation using four modules: (i) autotrophic respiration, (ii) phenological development, (iii) assimilate allocation and biomass growth, and (iv) biomass losses. They are described below. Equations, variables, parameters and initial values of the state variables are reported in Appendix A.

Two input datasets are needed to run the allocation module: (i) meteorological and environmental conditions (air temperature, soil temperature and soil relative extractable water, REW) and (ii) daily values of net canopy production. Temperatures were obtained from measurements at the study sites (see Sect. 2.3). Daily values of REW were estimated (Granier personal communication) by using a water balance model (Granier et al., 1999). Daily values of net canopy production were simulated with the FORUG model (see Sect. 2.2).

2.1.1 Autotrophic respiration

The maintenance and growth respiration of each organ is modelled separately. Maintenance respiration is calculated following Dufrêne et al. (2005) considering living biomass of the organ, basal respiration rates dependent on N content, and assuming an exponential relationship between respiration and temperature based on Q_{10} (i.e. the temperature response of respiration with a 10°C increase in temperature). Q_{10} is a function of temperature (Tjoelker et al., 2001). Growth respiration of each organ is proportional to the yield of growth processes (Thornley, 1970) specific for each organ and to the amount of C available for the growth of the respective organ.

2.1.2 Phenological development

We modelled 6 phenological stages: (1) Early spring – during this stage, leaves start to develop consuming C reserve. No growth or mortality of other organs occurs. This stage begins with budburst, depending on degree-days (Dufrêne et al., 2005), and lasts 10 days (Maillard et al., 1994; Barbaroux et al., 2003). (2) Late spring – during this stage leaves further develop, C reserves are refilled, and the growth of coarse roots, stems, and branches is initiated (Barbaroux and Bréda, 2002). The length of the late spring phase is 20 days (Maillard et al., 1994; Barbaroux et al., 2003). (3) Summer – during this stage, leaf biomass and area are at their annual maximal. All other organs grow and reserves accumulate (Barbaroux and Bréda, 2002). Mortality of fine roots takes place. (4) Early autumn – this stage corresponds to leaf yellowing, when non-structural leaf C is partly relocated to the C reserve (Hoffmann, 1995; Bossel, 1996). Growth and mortality of the other organs cease. This stage lasts 15 days (Hoffmann, 1995), starting when the 15-day gliding mean of canopy net primary production (NPP), drops below a threshold (NPP_{LY}). A similar method was used in the GROMIT model (Medlyn et al., 1999). (5) Late autumn – during this stage, leaf biomass is lost and C reserves are used to satisfy the tree C need. It lasts 35 days (Hoffmann, 1995). (6) Winter – the winter dormancy, maintained by the C reserves, lasts till budburst.

2.1.3 Assimilate allocation and biomass growth

This module is based on growth rules and source-sink relationships (Lacointe, 2000; Le Roux et al., 2001). Sources of assimilates are leaves (see Sect. 2.2) and C reserves. The sinks are fine roots, coarse roots, stems, and branches. The amount of assimilates supplied to these sinks is modelled according to (1) specific sink C demands, (2) sink hierarchy, (3) growth efficiency, and (4) allocation changes driven by the environment.

(1) Sink C demands. As reviewed by Le Roux et al. (2001), the assimilate demand of a sink has three elementary components: (i) maintenance respiration, (ii) growth, and (iii) C reserve storage. (i) Maintenance respiration is modelled as described in Sect. 2.1.1. (ii) The growth need of fine roots is modelled using a functional balance between fine roots and leaves. It depends on specific flush rates, current standing biomass, root-leaf ratio, and annual leaf biomass maximum (Bossel, 1996). In addition, the growth of fine root compensates for the fine root loss due to mortality (Bossel, 1996). The growth needs of coarse roots, stems, and branches are not specified in the model, but they equal the entire amount of assimilate left for wood growth. The C need

for sink growth varies according to the phenological stage; at the time the sink does not grow, its growth demand is assumed zero. (iii) Because of the scarce information about C reserve dynamics at the organ scale, the assimilate need for reserve storage is computed at the tree level. The C reserves are then distributed in fixed proportions among fine roots (8%), coarse roots (32%), stems (44%), and branches (16%) (Barbaroux et al. 2003). In CAF, the C need for reserve storage is computed similarly to the growth need.

(2) Sink hierarchy. The degree to which the sink C demands are satisfied depends on the amount of available assimilates and on the sink hierarchy. In CAF, fine roots have a higher priority than the woody compartments in the sink hierarchy. Because reserve storage was computed at the tree level (see above), the reserve pool was added to the hierarchy which is: (i) reserve, (ii) fine roots, and, on the same level, (iii) coarse roots, stems, and branches. Maintenance respiration is satisfied for every sink at any moment of the year. If the current photosynthates are insufficient to fulfil these needs, reserve assimilates are consumed. Conversely, if some of the current photosynthates remain after maintenance needs have been met, the reserve is supplied, followed by the fine roots, and finally the woody compartments (Lacointe, 2000). Actual priority order can differ from the sink hierarchy because the growth demand of a sink can be zero at specific time of the year (see above). An overview of the phenologically controlled source-sink hierarchical structure of CAF is given in Table 1.

(3) Growth efficiency. After the hierarchical allocation of the assimilates, a fraction of the C available for sink growth is incorporated as new biomass, whereas the remaining C is respired (see Sect. 2.1.1). The C allocated to wood growth is divided among coarse roots, stems, and branches using allometric ratios.

(4) Allocation changes driven by the environment. Temperature affects allocation by determining the amount of C invested in maintenance respiration (see Sect. 2.1.1) and the timing of leaf-bud burst (see Sect. 2.1.2). All meteorological conditions affecting photosynthesis (modelled with the FORUG model, see Sect. 2.2) indirectly affect also C allocation because they determine the end of the summer and onset of senes-

cence (see Sect. 2.1.2). Drought stress (arising when REW falls below 0.4; Granier et al., 1999) also affects photosynthesis and phenology. However, the direct effect that drought has on C allocation is more significant. Drought affects (i) fine root growth and mortality and (ii) the allocation between wood growth and reserve accumulation. (i) Fine root mortality is enhanced under drought stress (Hertel and Leuschner, 2002; Konôpka et al., 2005; Mainiero and Kazda, 2006 and reference therein). Beech reacts to this loss according to the intensity of the drought stress. If the stress is moderate, the enhanced fine root loss is fully compensated by enhanced fine root production (Hertel and Leuschner, 2002). If the stress is severe, fine root growth is ceased (Mainiero and Kazda, 2006). Thus, three responses are modelled for fine roots in case of drought: (a) an increase in fine root loss (50% increase, Hertel and Leuschner 2002), (b) an increase in fine root growth, in case of low-moderate drought (REW>0.2), to fully compensate for the increase in fine root loss, and (c) a cessation of fine root growth, in case of severe drought (REW<0.2). (ii) In moderately drought-tolerant species, wood growth slows or ceases under drought stress (Granier et al., 2000; Leuschner et al., 2001; Barbaroux and Bréda, 2002), whereas accumulation of non-structural C of reserve is less affected by water shortage (Barbaroux and Bréda, 2002). This agrees with basic physiological principles, indicating that growth is more sensitive to drought than photosynthesis and reserve storage (Cannell and Dewar, 1994; Würth et al., 2005 and references therein). Thus, two additional responses are modelled in case of drought: (d) a reduction in wood growth, and (e) an increase in reserve storage. This was modelled by transferring to the reserve part of the C normally allocated to wood growth (for details see Sect. 2.4 and equations in Appendix A).

2.1.4 Biomass losses

Biomass losses due to mortality are computed for fine roots, by using loss rates varying with phenology and current standing stocks (Bossel, 1996). Losses of coarse roots, stems, and branches are not modelled (the effects of wood turnover during a relatively short period, as the one considered in this study, are negligible). The loss of reserve assimilates occurs when the daily C gains are less than the maintenance C needs.

2.2 The FORUG model

FORUG is a process-based model that simulates CO_2 and H_2O exchange between even-aged forests and the atmosphere (Samson, 2001; Verbeeck et al., 2006, 2008). Processes of radiation interception, photosynthesis, rainfall interception and evapotranspiration are all simulated halfhourly. The canopy is divided in multiple layers composed of a sunlit and shaded fraction. In this study, the FORUG version described by Verbeeck et al. (2008) was used, with three modifications: (i) to take into account the effect of soil water stress on photosynthesis, the stomatal model was adapted following Leuning (1995) and Wang and Leuning (1998), using the soil water factor developed for the study site by Granier et al. (2000), (ii) the photosynthetic parameters V_{cmax} and J_{max} are calculated from leaf N content following Dufrêne et al., (2005), and (iii) net canopy production is obtained by subtracting leaf biomass production and leaf respiration from GPP, adding extra C from leaf relocation during early autumn. Leaf biomass production was simulated following Bossel (1996), using leaf development rates (Lebaube et al., 2000; Barbaroux and Bréda, 2002) and annual maximum leaf biomass derived from empirical values of maximum leaf area index ($\mathrm{LAI}_{\mathrm{max}}$, Granier personal communication) and specific leaf area (SLA, Bouriaud et al., 2003). Leaf growth- and maintenance respiration are modelled as described above for the other organs. The amount of C relocated during leaf yellowing is 10% of the annual maximum leaf biomass (Bossel, 1996). In case FORUG simulates a "negative" net canopy production (i.e. when the C need for leaf biomass production and leaf respiration is larger than the C supplied by the photosynthesis and leaf relocation), the pool of assimilate reserve in fine roots and wood is consumed.

When presenting the results of seasonal and interannual variations of C allocation and C pools, leaf biomass production and respiration calculated by FORUG were added (if appropriate) to the biomass production and respiration of the other organs to provide insight on the whole-stand dynamics.

2.3 Study site, study period, and meteorological-environmental datasets

The study site is a beech (*Fagus sylvatica* L.) stand situated in the forest of Hesse, France (48°40′N, 7°05′E; altitude of 300 m a.s.l.). The region has a semicontinental climate. Mean annual temperature and rainfall are 9.2°C and 820 mm, respectively. In 1997, the stand was 31 y old. It had a density of 4436 stems ha^{-1}, a mean height of 12 m, and a mean stem circumference of 22 cm. Understorey vegetation is sparse (Granier et al., 2000).

The study period ranges from 1997 to 2004. Datasets from 1997–1998 were used for model parameterization. Datasets from 1999–2004 were used to test and analyse the model results. Micrometeorological datasets used as inputs, were collected in the framework of the Euroflux, CarboEuroFlux, and CarboEurope-IP projects (Granier personal communiacation). An overview of the meteorological and drought conditions for 1999–2004 is shown in Table 2. Based on those data, 1999, 2000, and 2002 were considered as "wet" years (no drought), 2001 and 2004 as years with a low-moderate drought, and 2003 as a year characterized by a severe drought (Bréda et al., 2006).

2.4 Parameterization and sensitivity analysis

The 38 parameters of CAF were determined in four ways: (type 1 parameter) from measurement at the study site, (type 2) from measurements at comparable sites, (type 3) from typical values reported in the literature, and (type 4) obtained by model calibration. Calibration was straightforward and in three steps. First, the threshold for onset of autumn (NPP_{LY}) was optimized by minimizing the sum of squared errors between modelled and measured GPP for the period mid September–mid November 1997–1998. Second, fine root flush rate and fine root loss rate were optimized by forcing the model through measurements of fine root production in 1997 (Epron et al., 1999) and assuming the fine root stock at steady state. Finally, parameters describing C reserve dynamics were optimized by minimizing the sum of squared errors between modelled and measured stem C reserve content in 1998 (Barbaroux and Bréda, 2002).

The impact of the parameters on simulations was determined with a simple sensitivity analysis following Dufrêne et al. (2005). Accordingly, we compared a standard simulation with simulations performed with a +10% and −10% bias on every parameter. The maximum variation of C allocated annually to fine roots, structural wood, and C reserve, due to the two changes in parameter values (+10% and −10%), indicated the impact of the parameter.

2.5 Model testing

CAF was corroborated for the period 1999–2004 performing six tests. Simulations were compared with measurements of three important model outputs: (test 1) annual wood production, (test 2) standing above- and belowground wood, and (test 3) stem C reserve content. Annual wood production and standing wood biomass were obtained from annual biomass inventories (Granier personal communication), whereas data on stem C reserve were derived from Barbaroux and Bréda (2002) and Barbaroux et al. (2003). Goodness-of-fit was evaluated by determining regression slope, intercept, and explained variance (R^2). (test 4) The canopy production was tested by comparing modelled vs. measured growing season daily GPP and annual GPP. This test is important to check whether eventual discrepancies between modelled vs. measured C pool biomass are due to bias in simulating assimilation. GPP values for corroboration were calculated from measurements of NEE (collected with the eddy covariance technique within the Euroflux, CarboEuroFlux, and CarboEurope-IP projects; Granier personal communication), following Verbeeck et al. (2008). For this test, in addition to regression slope, intercept, and R^2 (see above), goodness-of-fit was evaluated by determining the systematic and unsystematic mean squared errors (MSE_s and MSE_u, respectively) (Kramer et al., 2002; Müller et al., 2005) for the regression between modelled vs. measured daily GPP. (test 5) The phenology was evaluated by comparing modelled vs. measured stem wood growth, derived from stem circumference increment (Granier personal communication). Finally, (test 6) in absence of time-series observations of respiration and fine root dynamics, the simulated 6-y mean (1999–2004) of aboveground wood maintenance respiration, root respiration, and fine root turnover were compared to measurements performed at the site in years different than the years used for parameterization.

3 Results

3.1 Model testing and sensitivity analysis

Simulated annual GPP did not differ more than 7% from the measurements, although the model slightly overestimated them (Table 3). Regression of modelled vs. measured annual GPP showed a slope and R^2 close to unity (1.03 and 0.90, respectively). Except for 2002, regressions of growing season modelled vs. measured daily GPP were close to the 1:1 line (slopes from 1.04 to 1.17; intercepts ranging from −0.0087 to −0.0003) and yielded fairly high R^2 (0.59–0.83) (Table 3). Correlation was lower in 2002 (slope: 0.76; intercept: 0.026; R^2: 0.50) (Table 3). Systematic errors were an order of magnitude lower than unsystematic errors (Table 3). Furthermore, FORUG reproduced well the seasonal pattern of measured GPP (Fig. 1).

Simulations of annual wood production were close to measurements. CAF slightly overestimated wood production in 2000 and 2004, whereas slightly underestimated it in the other years (Table 3). Mean difference between simulations and measurements was 10%. Regression of modelled vs. measured wood production had a slope of 0.77 and R^2 of 0.62. Regressions of modelled vs. measured below- and aboveground wood, in the 6-y study period, presented slopes of 1.05–1.07 and R^2 of 0.98. The seasonal pattern of stem growth was captured but simulated stem biomass lagged about 1 to 4 weeks behind measurements in spring (Fig. 2).

CAF overestimated C reserve during autumn-winter (11% as a mean), whereas it underestimated it during spring (40% as a mean) (Table 4). Differences were particularly high in April–June 1999 when the model overestimated C reserve consumption and simulations were only 45–50% of the measured reserve. Because of these last discrepancies, the regression of modelled vs. measured stem C reserve had a low R^2 (0.48) and high slope (1.50).

The 6-y mean of aboveground wood maintenance respiration ($1.56 \pm 0.09\,\mathrm{Mg\,C\,ha^{-1}\,y^{-1}}$), root respiration ($3.76 \pm 0.10\,\mathrm{Mg\,C\,ha^{-1}\,y^{-1}}$), and fine root turnover ($0.60 \pm 0.08\,\mathrm{y^{-1}}$) matched well experimental estimates ($1.54\,\mathrm{Mg\,C\,ha^{-1}\,y^{-1}}$, $4.0\,\mathrm{Mg\,C\,ha^{-1}\,y^{-1}}$, and $0.6\,\mathrm{y^{-1}}$, respectively; see: Epron et al., 1999; Le Goff and Ottorini, 2001; Damesin et al., 2002). Differences were lower than 10%.

The sensitivity analysis showed that parameters determining the sink C demand for growth and parameters of the maintenance respiration exhibited the largest impact on C allocation (see Table A3). Some parameters had a large impact on more than one C pool. The most important among these "crucial" parameters are the fine root-leaf ratio (λ_{RL}) and the maintenance respiration N dependency factor (MRN) (see Tables A2 and A3).

3.2 Seasonal C pool variations and C allocation pattern

The simulated seasonal variation of fine root- and wood standing biomass (Fig. 3) and the seasonality of C allocation among reserve, maintenance, and growth (Fig. 4) are described here in detail for 1999, together with data about leaf biomass and REW (Fig. 3). During the first four months of 1999 the stand was in winter dormancy, until budburst occurred on 2 May (day of the year, DOY, 122) (Fig. 3c). In winter none of the C pools showed any C accumulation. Wood C reserves were progressively consumed to satisfy the maintenance needs of the trees (Figs. 3a and 4a). Likewise, the decrease in fine root biomass was due to the consumption of the fraction of C reserve modelled to be stored in the fine root tissue (Fig. 3b). After budburst, reserves were massively consumed to sustain the growth of the new leaves, until they reached a minimum on 12 May (DOY 132) (Figs. 3c and 4a). Leaf growth was completed in late spring. During this period, canopy production fulfilled the overall tree maintenance and leaf growth, with extra assimilates available to immediately refill the reserves and initiate the growth of structural wood (Fig. 3a). However, the largest accumulation of C as structural wood occurred during the summer, concomitantly to the refilling of the C reserve (Figs. 3a and 4a). Fine root biomass showed a slight increase during late spring and early summer but slightly decreased for the rest of the growing season because of mortality (Fig. 3b). Loss of leaf biomass and relocation of leaf assimilates started on 7 October (DOY 280) (Fig. 3c). Relocation of leaf assimilates was reflected in an increase of the wood C reserve (Fig. 4a), which reached the annual maximum on 22 October (DOY 295) (Fig. 3a). In late autumn, relocation from senescent leaves, as well as any C accumulation, ceased, whereas C reserve begun to be consumed (Fig. 4c).

Very similar seasonal dynamics was simulated for the other years, with few exceptions. For instance, drought (especially if severe) affects seasonal variations of C pools and seasonality of C allocation because of the strong reduction in C assimilation it induces (Fig. 1). As a consequence, in late summer 2004 and, in particular, 2003 growth was substantially reduced and the C reserve was consumed to satisfy the tree maintenance (Fig. 4b). Interannual variability was also observed for the amplitude of the fine root increment in spring (Fig. 3f). Such increment depends on the functional balance between fine roots and leaves and the current fine root standing stock (see Eq. A5). Therefore, years with high leaf biomass (e.g. 2001) or low fine root biomass in early spring (e.g. 2004) showed large increment in fine roots. Conversely, years with high fine root mortality at the end of the growing season (e.g. the extremely dry 2003) showed at that time a large decline of fine root biomass (Fig. 3f).

3.3 Interannual C pool variations and C allocation pattern

The rate of ecosystem C cycling and the residence time of the C taken up by the ecosystem can be elucidated by analyzing (i) the proportion of C released by respiration vs. the proportion of C used for biomass production, and (ii) the proportion of C used for biomass production of fast-decomposing tree organs (or C pools) (leaves, fine roots, C reserve) vs. the proportion of C used for the production of slow-decomposing tree organs (coarse roots, stems, branches) (Fig. 5). Two distinct patterns in allocation

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appear. For wet years and years with low-moderate drought, the proportion of C used for biomass production is about the same of the one used for respiration (Fig. 5). Respiration was for about 70% due to maintenance and only 30% due to growth. On the other hand, for the hot and extremely dry 2003, a larger proportion of C was respired (+7%), particularly for maintenance, which accounted for about 80% of the total respiration. Furthermore, substantially lower production (of about 20–30%) was achieved in 2003 when compared to the other years (Fig. 5a). Annual allocation to wood and C reserve differs between wet and dry years. In wet years, the C allocated to wood and C reserve is 60–70% and up to 5%, respectively. Conversely, in dry years, those proportions are 45–50% and 5–10% (Fig. 5a). Allocation to fine root production is about 15–35%, without clear differentiation according to drought stress.

4 Discussion

4.1 Model testing and further model development

In general, annual and daily GPP are well reproduced, as well as the GPP seasonal pattern. Systematic errors were low, a proof that our model is not biased in a systematic way. The tendency of the model to slightly overestimate annual GPP and the poorer simulation for 2002 might be due to the photosynthetic parameters which were assumed constant for the entire study period without taking into account possible interannual variations (Verbeeck et al., 2008).

Discrepancies between modelled wood production and measurements were low. This is a relevant achievement. In CAF, wood has the lowest rank in the sink hierarchy and its growth occurs when all the other tree C needs are satisfied. Because no major flaws were found in estimating the annual GPP and the C needs of the other sinks, as well as wood maintenance respiration, a correct simulation of wood growth proves that the model captures well the annual vegetation C balance and C allocation pattern. Although some discrepancies in simulating wood increment in 2003 and 2004

(−10% and +16%, respectively), CAF captured to some extent also the time lag effect of the severe drought of 2003 on the wood growth of 2004 (Granier et al., 2007). Reduced wood growth in 2004 was mainly due to increased fine root production which compensated the high root die off of the previous very dry summer (Figs. 3f and 5a). Furthermore, the reduction in NPP simulated in 2003 (Fig. 5a), compares well with other model estimations (Ciais at al., 2005). Seasonality of wood growth was captured by CAF, but simulations lagged behind measurements in spring. This might indicate that wood growth starts immediately after budburst and not after a 10-day period as assumed in the model based on data of Barbaroux and Bréda (2002). In some years (e.g. 1999, 2003) this discrepancy was particularly pronounced because the lag in simulated stem growth was superimposed to some delay in simulated leaf budburst (Fig. 1).

During autumn and winter, simulated stem C reserve was close to measurements, but CAF underestimated reserves during spring, particularly during April–June 1999, when simulated reserves were about half of the measurements. This discrepancy might be due to two reasons. First, the proportion of reserve in stems and branches was assumed constant in the model. However, a higher proportion of reserve might be mobilized from the branches during leaf flush (Landhäusser and Lieffers, 2003), reducing the consumption of C reserve in stems. Second, the simulations might be improved by taking into account the “extra” assimilates from photosynthetic bark refixation (Barbaroux et al., 2003; Damesin, 2003). Damesin (2003) estimated that the C refixed during winter by current-year stems of beech is equivalent to about 7% of the total C reserve consumed by the trees from October till June, as measured by Barbaroux et al. (2003). Because older branch tissue can also have a high C refixation rate (Cernusak and Marshall, 2000), the actual C refixed by the entire crown might be much higher. In this study, an appropriate process-based modelling of these dynamics was precluded by a lack of detailed datasets of C reserve dynamics coupled to bark photosynthetic refixation.

Modelled mean of annual root respiration and aboveground wood maintenance respiration was very close to measurements. Comparisons with other observations confirm the reliability of our simulations. For instance, the simulated proportion of GPP used for aboveground respiration (30±1%) agrees very well with generic observations for European forest (29%, Janssens et al., 2001), whereas the simulated reduction in respiration in dry years and particularly in 2003 (−10% than 2002), agree with indications of Ciais et al. (2005) and Granier et al. (2007).

In summary, although caution should be taken when interpreting simulations of seasonality of C reserve and wood growth (see above), results showed that the model satisfactorily simulates the C fluxes of the processes most relevant for allocation dynamics: respiration and biomass production. The approach we used to simulate allocation based on growth-rules and source-sinks relationships proved therefore to be reliable. The large majority of the parameters used have a clear physiological meaning. Parameters obtained by calibration were few (7 out of 38) and, as shown by the sensitivity analysis, only three of them were important in the allocation procedure (see Table A3). The effects of environmentally-induced changes in modelling allocation (driven in particular by drought stress), coupled to the effects of environmentally-induced changes in modelling assimilation and respiration, gave rise to multiple feedbacks. For instance, high allocation to fine root production was observed not only in case of low-moderate drought (i.e. consistently to the modelling assumptions) but also in the year subsequent to a dry year, as 2002 and particularly 2004, because of the C investment needed to recover from reduction in fine roots during the previous season (Figs. 3f and 5a). On the other hand, wood production was similarly low in 2003 and 2004. However, in 2003 main constrain to wood growth was the drought-induced reduction in assimilation (Fig. 1), whereas in 2004 wood production was mostly limited by the high post-drought investment in fine roots (Fig. 5a). The appropriate simulation of these interconnected dynamics suggests the model to be flexible and able to simulate C allocation within a wide range of environmental conditions.

As it stands, the CAF model can be easily coupled to different types of canopy and NEE simulators to describe actual allocation patterns, growth dynamics, and C pool evolution in deciduous stands, and their interaction with the environment. In addition, the model could be used in dendroecology to analyse climate effects on growth by comparing ring-width series to model output as e.g. stem growth (Misson, 2004; Misson et al., 2004). Furthermore, CAF represents an ideal base upon which build whole-stand allocation models with predictive ability. Most important development to do so is the modelling of the canopy growth and, as major future challenge, the simulation of annual maximum leaf biomass (or area) and its interannual variability. Interannual leaf biomass and LAI variations in deciduous forests depend on numerous dynamics linked to both stand structure and tree physiological status. Thinning, previous year defoliation, -spring frost, and -drought, are some of its determinants (Bréda and Granier, 1996; Le Dantec et al., 2000; Barr et al., 2004; Krishnan et al., 2006). CAF is well suited for further implementation of these dynamics, e.g. the effect of drought on next year leaf biomass can be considered through its effect on tree C reserve (Le Dantec et al., 2000). A simple description of stand structure can be implemented also (Bossel, 1996). The development and corroboration of such integrated model will need extensive datasets describing comprehensively these interlinked dynamics. Today, needs of long-term datasets are most imminent for: (1) control of previous year C reserve on current growth of leaves and wood (Le Dantec et al., 2000; Bréda et al., 2006), (2) assessments of fine root growth and mortality, and their interaction with aboveground growth, and (3) monitoring of seasonal and interannual variations of canopy biomass and area as effected by biotic (e.g. fruiting, herbivory) and abiotic (e.g. drought) effects.

4.2 Interannual C pools variations

In this study, we made use of the process-based characteristics of our model to deepen our knowledge on stand C allocation dynamics. This was achieved by (i) integrating different tree physiological processes (assimilation, maintenance, growth, reserve storage and consumption) and tree organs (fine roots, coarse roots, stems, branches), and (ii) resizing the time-scale of available empirical information from e.g. monthly or annually to daily (i.e. the time step of CAF). In other words, we employed a model to extend existing datasets of ecosystems dynamics (McKane et al., 1997), giving a unitary frame to a large amount of more fragmented experimental information. In particular, we analyzed the C allocation pattern in a beech stand as effected by meteorological (e.g. air temperature) and environmental variability (e.g. soil water status) during six years.

At annual and interannual scale, simulation of C allocation allows gaining key information about the fate of C in the ecosystem and it can substantially improve our long-term predictions of ecosystem C storage capacity and C cycling rate. We found that 45–70% of the C allocated annually to biomass production at the site was stored as wood (a slowly-decomposing long-term C pool), whereas 15–35% and up to 11% was stored as fine roots, and C reserve, respectively (fast-decomposing short-term C pools). The remaining 10–25% of C was allocated to leaf production, as derived from experimental data.

The effects of summer drought on C allocation can be confused with the effects caused by high temperature, because summer droughts occur often in concomitance to warm periods or heat waves, as in 2003 (Table 2). However, model tests with high summer temperature not concurrent to drought (and vice versa) showed that increased summer temperature increases maintenance respiration (10% in case of an increment of 4°C per day during July, August and September) but has negligible effect on total biomass production (1% reduction) and C allocation (data not shown). On the other hand, drought has a substantial effect on biomass production and allocation because its negative effect on photosynthesis and growth, independently on temperature. Indeed, a considerably different allocation pattern was observed between years with and without drought, independently on temperature. For example, we found that a higher proportion of C was allocated to the fast-decomposing C pools (C reserve, fine roots and leaves) in the moderately dry 2004 than in the wet 1999 (55% vs. 33%), and logically the reverse was true for the proportion of C allocated to the slowly-decomposing C pools (wood) (45% vs. 67%). Although the amount of C invested in biomass in these two years was very similar (Fig. 5a), the residence time of the C stored in the ecosystem differs. Considering the entire study period, the proportion of C allocated to fast-decomposing C pools increased by +13% in case of severe drought and by an average of +18% in case of low to moderate drought. Thus, drought not only decreases net primary production (Ciais et al., 2005), but increases ecosystem C cycling rate, by increasing the stocks of fast-decomposing vs. slowly-decomposing C pools. This highlights the importance of modelling C allocation in forest ecosystems, particularly in those regions expected to experience more frequent droughts in the coming decades (Gregory et al., 1997).

Appendix A

Equations and sensitivity analysis of the CAF model

Autotrophic respiration

(1) maintenance respiration

$$r_{mP}=\sum_{n=1}^{\text{tsd}}\text{sts}\cdot P\cdot LB_P\cdot N_P\cdot \text{MRN}\cdot Q_{10P}^{(T-15)/10} \qquad \text{Dufrêne et al. (2005)} \qquad \text{(A1)}$$

with

$$Q_{10P}=a_P\cdot T+b_P \qquad \text{Tjoelker et al. (2001)} \qquad \text{(A2)}$$

$$a_{\text{resp}}=r_{mR}+r_{mS}+r_{mB}+r_{mU} \qquad \text{(A3)}$$

with tsd number time steps per day (usually 48) and sts number second per time step (usually 1800). Equations (A1) and (A2) apply to any tree organ (or C pool, P). The entire fine root biomass is considered to respire.

(2) growth respiration

$$r_{gP}=a_{gP}\cdot(1-Y_{GP}) \tag{A4}$$

Assimilate allocation and biomass growth

(1) sink C demand for growth

$$r_{\mathrm{dem}}=\begin{cases} r_{\mathrm{loss}}+\rho_{\mathrm{flush}R3}\cdot(\lambda_{RL}L_{\mathrm{max}}-W_R) & \text{if} \quad \text{stage}=3 \\ 0 & \text{if} \quad \text{stage}\neq 3 \end{cases} \qquad \text{Bossel (1996)} \tag{A5}$$

$$w_{\mathrm{dem}}=a_gW\cdot(1-\lambda_{AR}) \quad \text{with} \begin{cases} \lambda_{AR}=0 & \text{if} \quad \text{stage}=2 \text{ or stage}=3 \text{ and REW}>0.4 \\ \lambda_{AR}=0.25 & \text{if} \quad \text{stage}=3 \text{ and REW}\leq 0.4 \end{cases} \tag{A6}$$

(2) C demand for storage of assimilates of reserve

$$ar_{\mathrm{dem}}=\begin{cases} \rho_{\mathrm{storage2}}\cdot(AR_{\mathrm{max}}-AR) & \text{if} \quad \text{stage}=2 \\ \rho_{\mathrm{storage3}}\cdot(AR_{\mathrm{max}}-AR)+a_{gW}\cdot\lambda_{AR} & \text{if} \quad \text{stage}=3 \\ a_{gAR} & \text{if} \quad \text{stage}=4 \text{ or } 5 \\ 0 & \text{if} \quad \text{stage}=1 \text{ or } 6 \end{cases} \tag{A7}$$

with

$$AR_{\mathrm{max}}=\iota\cdot(W_R+W_S+W_B+W_U) \tag{A8}$$

AR_{max} is only used to calculate ar_{dem} during stages 2 and 3. During other periods or under drought stress, actual values of AR may be higher than AR_{max}.

(3) growth efficiency

$$r_{\mathrm{grow}}=\begin{cases} Y_{GR}\cdot r_{\mathrm{dem}} & \text{if} \quad a_{gR}\geq r_{\mathrm{dem}} \\ Y_{GR}\cdot a_{gR} & \text{if} \quad a_{gR}<r_{\mathrm{dem}} \end{cases} \tag{A9}$$

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$$w_{U\,\mathrm{grow}}=Y_{GU}\cdot a_{gW}\cdot\lambda_U \tag{A10}$$

$$w_{S\,\mathrm{grow}}=Y_{GS}\cdot a_{gW}\cdot(1-\lambda_B-\lambda_U) \tag{A11}$$

$$w_{B\,\mathrm{grow}}=Y_{GB}\cdot a_{gW}\cdot\lambda_B \tag{A12}$$

Standing pool biomass (P) and daily variation of standing pool biomass (ΔP) are calculated as follows:

$$\Delta P=p_{\mathrm{grow}}-p_{\mathrm{loss}} \tag{A13}$$

$$P=P_{d-1}+\Delta P \tag{A14}$$

where P_{d-1} is the value of standing pool biomass on the previous day.

Biomass losses

$$r_{\mathrm{loss}}=\begin{cases}\rho_{R3}(1+\zeta_R)W_R & \text{if}\quad \text{stage}=3\\ 0 & \text{if}\quad \text{stage}\neq 3\end{cases}\qquad \text{Bossel (1996)} \tag{A15}$$

$$ar_{\mathrm{loss}}=\begin{cases}0 & \text{if}\quad a_{\mathrm{prod}}>a_{\mathrm{resp}}\\ a_{\mathrm{resp}}-a_{\mathrm{prod}} & \text{if}\quad a_{\mathrm{prod}}<a_{\mathrm{resp}}\end{cases} \tag{A16}$$

where a_{prod} is the net canopy production simulated by the FORUG model (see Sect. 2.2).

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Table 1. Phenologically driven source-sink hierarchical structure of CAF.

tree organ or C pool		rank	phenological phase[a]					
			1	2	3	4	5	6
sources	leaves	1	○	●	●	●	●	○
	reserve (consumption)	2	●	●	●	●	●	●
sinks	reserve (storage)	1	○	●	●	●	●	○
	fine roots	2	○	○	●	○	○	○
	coarse roots	3	○	●	●	○	○	○
	stems	3	○	●	●	○	○	○
	branches	3	○	●	●	○	○	○

solid circle: the source or sink is active; open circle: the source or sink is inactive.

[a] phenological phases: (1) early spring, (2) late spring, (3) summer, (4) early autumn, (5) late autumn, and (6) winter.

Table 2. Meteorological conditions and soil drought stress during the whole year and summer time (July–August–September) for the period 1999–2004 at Hesse (data from Granier personal communication).

variable	1999	2000	2001	2002	2003	2004
mean annual temperature (°C)	10.1	10.9	10.0	10.5	10.7	9.7
mean temperature July–September (°C)	17.8	16.5	16.6	16.1	19.2	17.2
accumulated annual precipitation (mm)	1111	1023	1151	1158	661	914
accumulated precipitation July–September (mm)	267	363	344	290	134	214
start of water stress[a] (DOY)	n.ws.	n.ws.	180	n.ws.	173	179
water stress duration[a] (days)	0	0	71	0	130	101
drought intensity index[a] (no units)	0	0	11	0	77	34

n.ws.: year without water stress.

[a] according to Bréda et al. (2006).

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Table 3. Modelled and measured gross primary production (GPP) and wood production for the beech stand of Hesse during 1999–2004. Statistical parameters of the regression modelled vs. measured daily GPP refer to the growing season only (experimental data from Granier personal communication).

year	annual GPP (Mg C ha^{-1} y^{-1})		growing season daily GPP regression parameters					wood production (Mg C ha^{-1} y^{-1})	
	modelled	measured	slope	intercept	R^{2a}	MSE$_u$(10^{-5})^a	MSE$_s$(10^{-5})^a	modelled	measured
1999	15.1	14.2	1.09	−0.0016	0.72	61.1	3.5	5.2	5.3
2000	16.8	16.0	1.17	−0.0087	0.83	38.2	6.2	5.5	4.6
2001	16.1	16.0	1.04	−0.0029	0.70	75.3	0.3	4.4	4.5
2002	17.5	16.3	0.76	0.0256	0.50	114.0	15.3	4.9	5.2
2003	14.2	13.6	1.07	−0.0011	0.75	69.6	2.5	3.7	4.1
2004	15.3	14.8	1.04	−0.0003	0.59	79.3	1.1	3.6	3.1

[a] R^2 (explained variance), MSE$_u$ (unsystematic mean squared error) and MSE$_s$ (systematic mean squared error) are all significant ($p<0.0001$).

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Table 4. Modelled and measured C reserve of stems at the beech stand of Hesse during 1999–2000 (experimental data from Barbaroux and Bréda, 2002; Barbaroux et al., 2003)

day	stem C reserve (Mg C ha^{-1}) modelled	 measured
3 February 1999	0.57	0.53
27 April 1999	0.32	0.60
1 June 1999	0.29	0.67
14 October 1999	0.92	0.90
3 November 1999	0.92	0.75
4 June 2000	0.59	0.70

Table A1. Variables of the CAF model (see Eqs. A1–A16).

symbol	variable	units
State variables		
AR	Assimilates reserve	Mg C ha^{-1}
W_R	Fine root carbon biomass	Mg C ha^{-1}
W_B	Branch carbon biomass	Mg C ha^{-1}
W_S	Stem carbon biomass	Mg C ha^{-1}
W_U	Coarse root (underground wood) carbon biomass	Mg C ha^{-1}
Maintenance respiration		
a_{resp}	Stand maintenance respiration	Mg C ha^{-1} day^{-1}
r_{mR}	Maintenance respiration fine roots	Mg C ha^{-1} day^{-1}
r_{mB}	Maintenance respiration branches	Mg C ha^{-1} day^{-1}
r_{mS}	Maintenance respiration stems	Mg C ha^{-1} day^{-1}
r_{mU}	Maintenance respiration coarse roots	Mg C ha^{-1} day^{-1}
T	Air temperature	°C
Q_{10R}	Temperature response of fine root respiration	dimensionless
Q_{10B}	Temperature response of branch respiration	dimensionless
Q_{10S}	Temperature response of stem respiration	dimensionless
Q_{10U}	Temperature response of coarse root respiration	dimensionless
Growth respiration		
a_{gAR}	Assimilates available for reserve accumulation	Mg C ha^{-1} day^{-1}
a_{gR}	Assimilates available for fine root growth	Mg C ha^{-1} day^{-1}
a_{gW}	Assimilates available for wood growth	Mg C ha^{-1} day^{-1}
r_{gR}	Growth respiration fine roots	Mg C ha^{-1} day^{-1}
r_{gB}	Growth respiration branches	Mg C ha^{-1} day^{-1}
r_{gS}	Growth respiration stems	Mg C ha^{-1} day^{-1}
r_{gU}	Growth respiration coarse roots	Mg C ha^{-1} day^{-1}

Table A1. Continued.

symbol	variable	units
Sink C demand for growth		
ar_{dem}	Demand for assimilate reserve storage	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
AR_{max}	Assimilate reserve maximum	$\mathrm{Mg\,C\,ha^{-1}}$
r_{dem}	Fine root demand for growth	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
w_{dem}	Wood demand for growth	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
Growth efficiency		
ar_{grow}	Accumulated assimilates of reserve	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
r_{grow}	Newly grown fine root biomass	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
w_{Bgrow}	Newly grown branch biomass	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
w_{Sgrow}	Newly grown stem biomass	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
w_{Ugrow}	Newly grown coarse root biomass	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$
Biomass losses		
r_{loss}	Fine root loss	$\mathrm{Mg\,C\,ha^{-1}\,day^{-1}}$

Table A2. Parameters and initial values of the state variables of the CAF model used in this study (see Eqs. A1–A16). The parameters are classified as: (type 1) parameters measured at the study site, (type 2) parameters measured at comparable sites, (type 3) parameters with typical value from the literature, and (type 4) parameters obtained by calibrating the model.

symbol	units	parameter	value	reference	type
Maintenance respiration					
a_R	dimensionless	Slope function Q_{10} vs. temp. for fine roots	−0.042	Tjoelker et al. (2001)	3
a_B	dimensionless	Slope function Q_{10} vs. temp. for branches	−0.046	Tjoelker et al. (2001) (slope as leaves)	3
a_S	dimensionless	Slope function Q_{10} vs. temp. for stems	−0.046	Tjoelker et al. (2001) (slope as leaves)	3
a_U	dimensionless	Slope function Q_{10} vs. temp. for coarse roots	−0.042	Tjoelker et al. (2001) (slope as fine roots)	3
b_R	dimensionless	Intercept function Q_{10} vs. temp. (fine roots)	2.83	Epron and Badot,(1997); Tjoelker et. al.,(2001)	3
b_B	dimensionless	Intercept function Q_{10} vs. temp. (branches)	3.49	Damesin et al.,(2002); Tjoelker et al.,(2001)	3
b_S	dimensionless	Intercept function Q_{10} vs. temp. (stems)	2.39	Damesin et al.,(2002); Tjoelker et al.,(2001)	3
b_U	dimensionless	Intercept function Q_{10} vs. temp. (coarse roots)	2.33	Damesin et al.,(2002); Tjoelker et al.,(2001)	3
LB_B	dimensionless	Fraction living cells in branches	0.327	Ceschia et al.,(2002)	1
LB_S	dimensionless	Fraction living cells in stems	0.206	Ceschia et al.,(2002)	1
LB_U	dimensionless	Fraction living cells in coarse roots	0.206	assumed equal to LB_S	3
MRN	$\mathrm{mol\,CO_2\,g^{-1}\,N\,h^{-1}}$	Nitrogen dependency for all organs	$5.5\,10^{-4}$	Dufrêne et al. (2005)	3
N_R	$\mathrm{mg\,N\,g^{-1}\,DM}$	Nitrogen content of fine roots	9.99	van Praag et al. (1988)	2
N_B	$\mathrm{mg\,N\,g^{-1}\,DM}$	Nitrogen content of branches	3.3	Ceschia et al. (2002)	1
N_S	$\mathrm{mg\,N\,g^{-1}\,DM}$	Nitrogen content of stems	1.2	Ceschia et al. (2002)	1
N_U	$\mathrm{mg\,N\,g^{-1}\,DM}$	Nitrogen content of coarse roots	1.2	assumed equal to N_S	3
ς_{CR}	$\mathrm{g\,C\,g^{-1}\,DM}$	Fine root carbon content	0.48	Barbaroux et al. (2003)	1
ς_{CB}	$\mathrm{g\,C\,g^{-1}\,DM}$	Branch carbon content	0.47	Barbaroux et al. (2003)	1
ς_{CS}	$\mathrm{g\,C\,g^{-1}\,DM}$	Stem carbon content	0.46	Barbaroux et al. (2003)	1
ς_{CU}	$\mathrm{g\,C\,g^{-1}\,DM}$	Coarse root carbon content	0.48	Barbaroux et al. (2003)	1

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Table A2. Continued.

symbol	units	parameter	value	reference	type
Growth respiration					
Y_{GR}	g C new mass g^{-1} C substrate	Yield of growth of fine roots	0.787	Rambal et al. (2004)	2
Y_{GB}	g C new mass g^{-1} C substrate	Yield of growth of branches	0.725	assumed equal to Y_{GS}	3
Y_{GS}	g C new mass g^{-1} C substrate	Yield of growth of stems	0.725	Damesin et al. (2002)	1
Y_{GU}	g C new mass g^{-1} C substrate	Yield of growth of coarse roots	0.725	assumed equal to Y_{GS}	3
Phenology					
N_{startBB}	Julian day	Date of onset of rest	25	Dufrêne et al. (2005)	2
T_{BB}	°C	Base temperature for forcing budburst	1	Dufrêne et al. (2005)	2
F_{critBB}	°C	Threshold for budburst	580	Dufrêne et al. (2005)	2
NPP_{LY}	μmol CO$_2$ m^{-2} s^{-1}	Threshold canopy net primary production	1	parameterization	4
Sink C demand for growth					
ι	g C reserve g^{-1} C biomass	Tree reserve maximum concentration	0.039	parameterization	4
λ_{AR}	dimensionless	Carbon fraction relocated to reserve	0.25	parameterization	4
λ_{RL}	dimensionless	Fine root-leaf ratio	2.1	derived from Bartelink (1998)	2
ρ_{flushR3}	day^{-1}	Fine root flush rate stage 3	1	parameterization	4
ρ_{storage2}	day^{-1}	Rate of carbon reserve storage at stage 2	0.015	parameterization	4
ρ_{storage3}	day^{-1}	Rate of carbon reserve storage at stage 3	0.045	parameterization	4
Growth					
λ_B	g C branches g^{-1} C wood	Ratio of branches to total wood biomass	0.13	Granier (personal communication)	1
λ_U	g C coarse roots g C^{-1} wood	Ratio of coarse roots to total wood biomass	0.29	Granier (personal communication)	1

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symbol	units	parameter	value	reference	type
Biomass losses					
ρ_{R3}	day^{-1}	Fine root loss rate stage 3	0.004	parameterization	4
ζ_R	dimensionless	Fine root loss rate increase due to drought	0.5	derived from Hertel and Leuschner (2002)	2
Initial values of the state variables					
AR	Mg C ha^{-1}	Assimilate reserve	1.62	derived from Barbaroux et al. (2003)	–
W_R	Mg C ha^{-1}	Fine root carbon biomass	3.31	Epron et al. (1999)	–
W_B	Mg C ha^{-1}	Branch carbon biomass	6.09	Granier (personal communication)	–
W_S	Mg C ha^{-1}	Stem carbon biomass	26.05	Granier (personal communication)	–
W_U	Mg C ha^{-1}	Coarse root carbon biomass	14.35	Granier (personal communication)	–

Table A3. Results of the sensitivity analysis. Effect of parameters of CAF on the amount of C allocated annually to C reserve (*AR*), structural wood (*W*), and fine roots (W_R), when a variation of (+ and −) 10% is applied to each parameter (for each parameter the highest effect generated by the two variations is considered). The 10 parameters with the largest effect on allocation are shown (most important four parameters for each pool are in parenthesis with rank). Parameters were determined in four ways: (type 1) from measurement at the study site, (type 2) from measurements at comparable sites, (type 3) from typical values reported in the literature, and (type 4) obtained by model calibration.

parameter	description	module	type	effect on model output (%)		
				AR	*W*	W_R
λ_{RL}	Fine root-leaf ratio	growth demand	2	9.2 (3)	6.7 (2)	35.8 (1)
MRN	Nitrogen dependency for all organs	maintenance respiration	3	15.1 (2)	8.8 (1)	5.2 (2)
ι	Tree reserve maximum concentration	growth demand	4	18.7 (1)	0.3	0.7
F_{critBB}	Threshold for budburst	phenology	2	5.8	6.1 (3)	0.2
ς_{CR}	Fine root carbon content	maintenance respiration	1	6.2 (4)	3.9	1.9
N_R	Nitrogen content of fine roots	maintenance respiration	2	5.6	3.5	1.7
ρ_{R3}	Fine root loss rate stage 3	relocation and loss	4	3.2	2.9	4.5 (3)
Y_{GR}	Yield of growth of fine roots	growth respiration	2	3.7	3.1	2.2 (4)
Y_{GS}	Yield of growth of stems	growth respiration	1	2.7	5.5 (4)	0.2
λ_{RL}	Carbon fraction relocated to reserve	growth demand	4	5.9	0.2	0.2

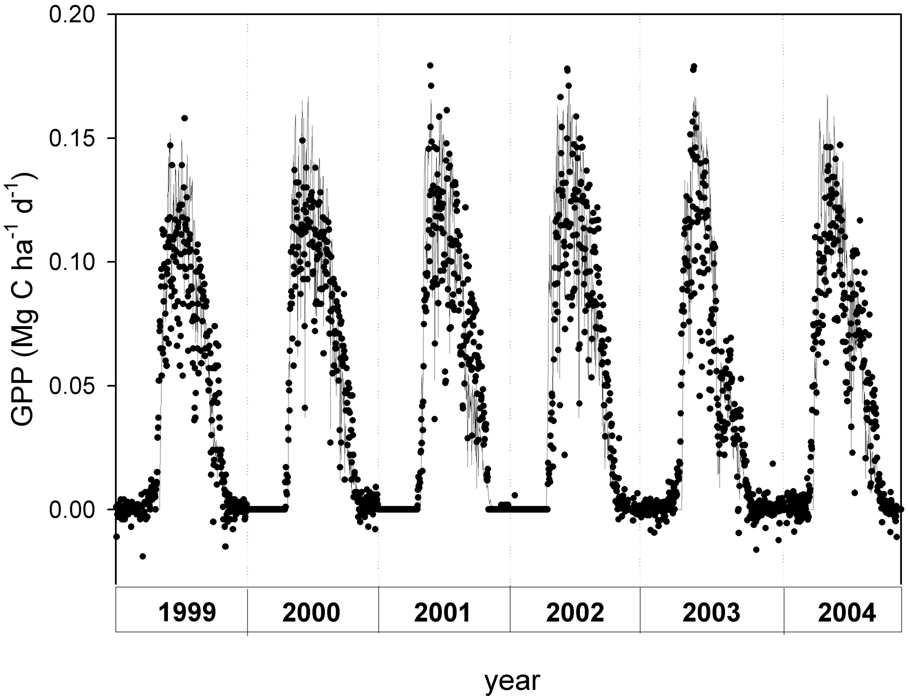

Fig. 1. Modelled (–) vs. measured (•) daily gross primary production (GPP) at the beech stand of Hesse during 1999–2004 (experimental data from Granier personal communication).

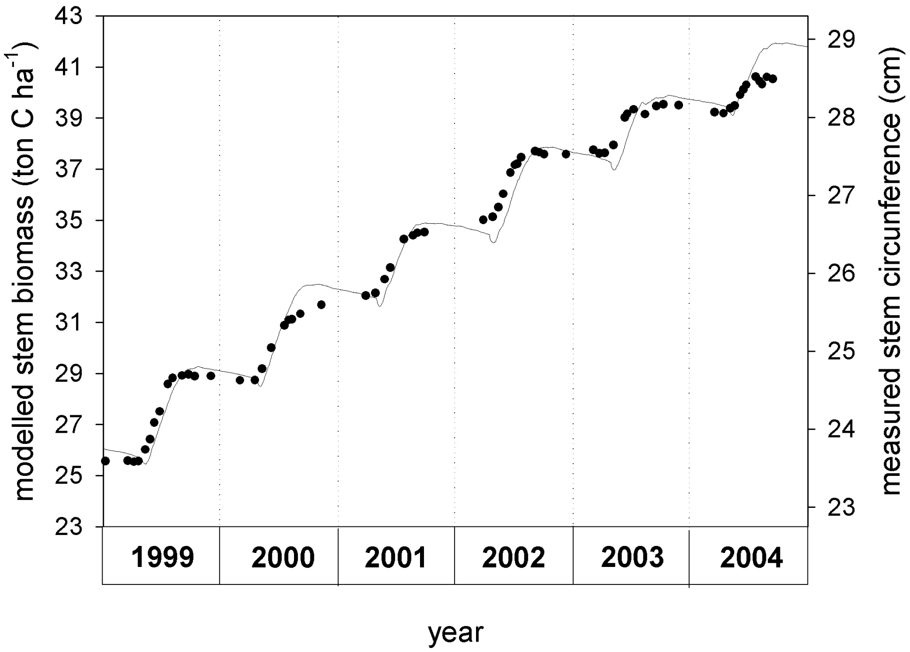

Fig. 2. Modelled stem biomass (–) and measured mean stem circumference (•) during 1999–2004 at the beech stand of Hesse (experimental data from Granier personal communication), (stem biomass decline in winter is due to consumption of stem C reserves; see text).

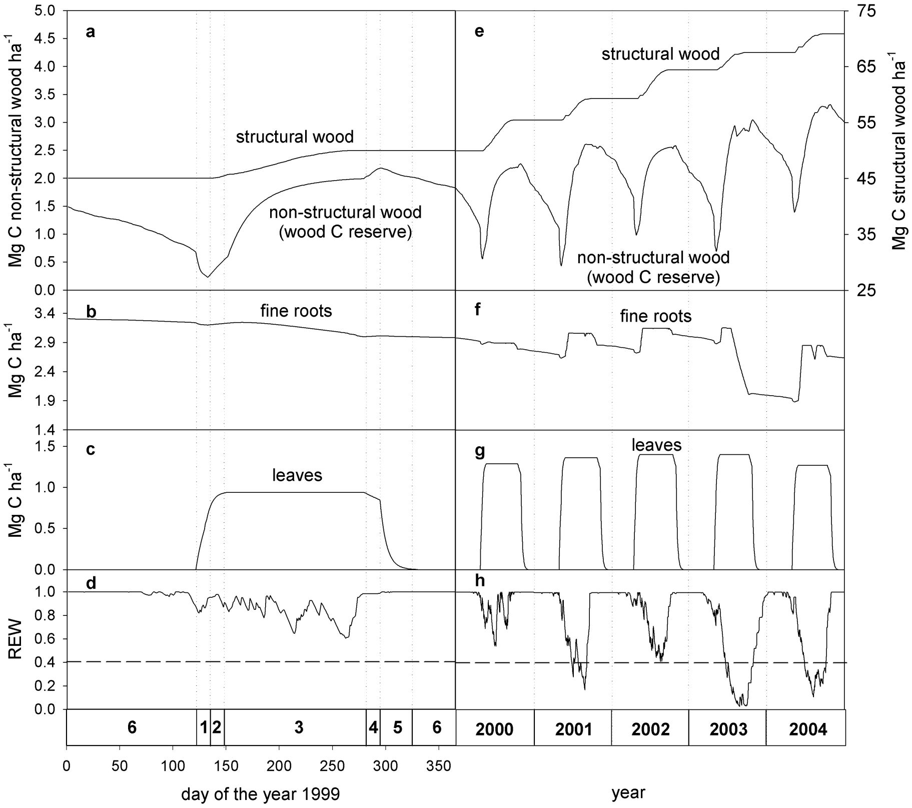

Fig. 3. Simulated seasonal variations of fine roots and (structural and non-structural) woody biomass in comparison with seasonal variations of leaf biomass and relative extractable water (REW) (Granier personal communication), for the beech stand of Hesse in the period 1999–2004. Drought stress occurs at REW below the threshold 0.4 (Granier et al. 1999). Simulations for 1999 are plotted against the phenological stages (1: early spring; 2: late spring; 3: summer; 4: early autumn; 5: late autumn, and 6: winter).

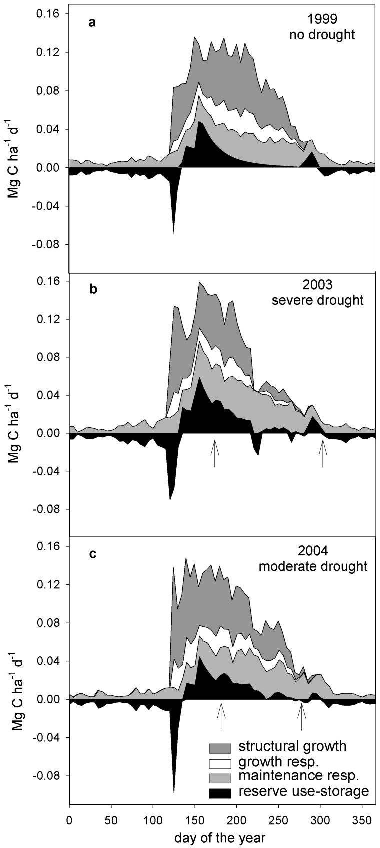

Fig. 4. Seasonal course of assimilate allocation among reserve, maintenance respiration, growth respiration and structural growth, and seasonal course of C reserve consumption simulated for the beech stand of Hesse during **(a)** 1999 (a year without drought), **(b)** 2003 (a year with severe drought), and **(c)** 2004 (a year with moderate drought). Arrows indicate start and end of the drought period.

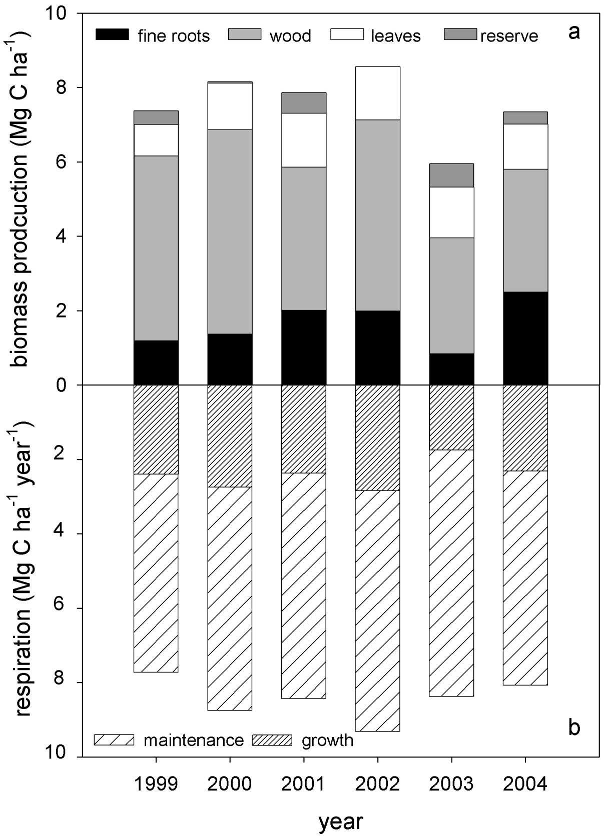

Fig. 5. Fate of C taken up annually at the beech stand of Hesse during the period 1999–2004: **(a)** biomass production, expressed as the sum of (modelled) fine root-, wood- and C reserve production plus (empirical) leaf production, and **(b)** respiration, expressed as sum of (modelled) maintenance- and growth respiration.