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Modelling carbon and water cycles in a beech forest Part II.: Validation of the main processes from organ to stand scale

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Abstract

A forest ecosystem model (CASTANEA) simulating the carbon balance (canopy photosynthesis, autotrophic and heterotrophic respirations, net ecosystem exchange, wood and root growth) and the water cycle (transpiration, soil evaporation, interception, drainage and soil water status) is tested with data from a young beech forest (*Fagus sylvatica* L.). For this purpose, the model validity is assessed by comparison between net CO_2 and H_2O fluxes simulated and measured by the eddy flux technique over one year. In addition, most of the sub-models describing the processes mentioned above are tested using independent measurements from the same forest stand: tree growth, branch photosynthesis, wood and soil respirations, sap flow and soil water content. Most of the input parameters (both weather and plant characteristics) are measured in the same experimental site (i.e. Hesse forest) independently of the validation dataset (none has been fitted to match the output data, except rainfall interception parameters); some are from other beech sites or from literature. Concerning the radiative transfer, the model reproduces the measured exponential PAR extinction and provides a good estimate of the net radiative budget, except during winter. At the branch scale, simulated photosynthesis and transpiration of sun-leaves are close to the measurements. We show also, using model simulations, that the seasonal decrease of measured net photosynthesis at the branch level could be explained by a decrease in leaf nitrogen content during the leafy season. At stand scale, a good correlation was obtained between simulated and observed fluxes both on a half-hourly basis and on a daily basis. Except at the end of the leafy season, the model reproduces reasonably well the seasonal pattern of both CO_2 and H_2O fluxes. Finally, even if there are some discrepancies between model estimations and fluxes measured at stand scale by eddy covariance, the model simulates properly both annual carbon and water balances when compared with the sum of the measured local fluxes. The remaining differences question the scaling up process when building such a model and the spatial footprint of eddy fluxes measurements.

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1. Introduction

In the recent years, several research programs monitor CO_2 and H_2O fluxes above temperate, boreal and also tropical forest canopies. A global network (FLUXNET) of over 250 long-term eddy flux stations exists (Running et al., 1999; Baldocchi et al., 2001a) and the number of stations is rapidly increasing. Many studies have shown a strong variability in the net ecosystem exchange of the carbon (NEE) according to water availability, species composition or environmental characteristics (Law et al., 2002). Process-based models provide a theoretical framework for analysis and interpretation of the scaling of physiological processes, enabling physiologists to extend their work to larger scales (De Pury and Farquhar, 1997). They then allow us to improve our understanding of measured NEE variability and to predict the global change effect. With the increase of longer data sets, there is a new challenge for testing coupled carbon–water flux models on multi-time and spatial scales. Some works have been made in this direction (Aber et al., 1996; Grant et al., 1999; Kimball et al., 1999; Law et al., 2000a,b; Baldocchi and Wilson, 2001b) but often by using only integrative measurements by the eddy covariance method. But recently, some studies have shown that there were some discrepancies between integrative fluxes measurements and other independent measurements of NEE (Granier et al., 2000a; Ehman et al., 2002).

Moreover, if one intends to predict both short-term and long-term net ecosystem exchanges dynamics in forests, a canopy carbon–water flux model must be coupled with a biogeochemical model including carbohydrates allocation, growth and maintenance respiration, litter production and mineralisation, soil organic matter mineralisation and soil water balance sub-models. These models include a large number of parameters and variables linked together in different sub-models running at different time steps and different spatial scales.

Consequently, there is a necessity to test these assembling of sub-models using not only integrative data sets at the ecosystem scale (NEE, evapotranspiration (ETR)) but also data from different compartments of the system (soil respiration, soil water content, tree ring increment, organ growth, wood respiration, etc.). According to the difficulties of some measurements, these data sets are not common and rarely available for the same stand.

We then developed a new hybrid model, CASTANEA, described in Dufrêne et al. (2005) aiming to capture net carbon and water fluxes of deciduous forests from half-hourly to multi-annual time scales and to accurately simulate ecosystem changes in biomass and soil organic matter from season to decades. The objectives of this research are to quantify how fluxes (CO_2, H_2O) and carbon pools (trunks and soil organic matter) in a temperate beech forest vary across these multiple scales and how climate, dynamic plant structure and physiological capacity act upon these variables.

In this paper, we focus on the validation of the different sub-models: light interception, branch photosynthesis, leaf and wood respiration, soil autotrophic and heterotrophic respiration, transpiration, rainfall interception, soil water content, tree growth, NEE. Because of the large number of variables and parameters included in this type of process-based models it is very difficult to validate the outputs using only the few synthetic variables generally available (NEE, ETR). Consequently, our approach was to test separately the most important sub-models included in CASTANEA using a large data set from a temperate beech forest located in Hesse (North-East of France) over one year. Then, we compare three independent annual ecosystem carbon balances: (1) estimated by the eddy covariance method, (2) estimated by the sum of the measurements of each individual process, and (3) simulated by the model. This work can both provide an independent evaluation of tower-based flux measurements and a reliable validation of a process-based model in order to use it with confidence to address other questions. For example, CASTANEA has already been used to evaluate the annual productivity and carbon fluxes over a large heterogeneous forest region (over 17,000 ha), in terms of species composition, canopy structure, age, soil type and water and mineral resources (le Maire et al., 2005). CASTANEA is also designed to quantify the relative effects of global changes (CO_2, temperature, precipitation, radiation, etc.) on forest growth during last century.

2. Synthetic model description

CASTANEA is a physiologically multi-layer process-based model aiming to predict the carbon

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balance of an even-aged monospecific deciduous forest stand. The main output simulated variables are (i) the evolution of leaf area index, the standing biomass, the soil carbon and water content which are state variables, and (ii) the canopy assimilation, the maintenance and growth respirations, growth of organs, soil heterotrophic respiration, transpiration and evapotranspiration which are flux densities variables.

The canopy is assumed to be homogeneous horizontally and vertically subdivided into a variable number of layers (i.e. multi-layer canopy model), each of them enclosing the same amount of leaf area (typically less than $0.1\,m^2\,m^{-2}$). No variability between trees is assumed and then one "averaged" tree is considered to be representative of the stand. Tree structure is a combination of five functionally different parts: foliage, stems, branches, coarse and fine roots. A carbohydrate storage compartment is also considered but is not physically located in the model.

Half-hourly rates of gross canopy photosynthesis and transpiration are calculated from incident radiation and photosynthetic characteristics of individual leaves. Leaf nitrogen per unit area ($gN\,m^{-2}$ leaf) is calculated from measured leaf nitrogen concentration ($gN\,g_{dm}{}^{-1}$ leaf), which is assumed to be constant inside the canopy, multiplied by the leaf mass per area, which decreases exponentially inside the canopy. The photosynthetic capacity of leaves, in different positions inside the canopy, is derived from leaf nitrogen density.

After subtraction of maintenance respiration requirements, the remaining assimilates are allocated to the growth of various plant tissues using a priority system, which varies according to the season. Phenological stages (budburst, end of leaf growth, start of leaf yellowing, etc.) and leaf growth are based on day-degrees. Maintenance respiration depends on temperature and nitrogen content of various organs while growth respiration depends on the biochemical composition of the considered organs.

The soil water balance is assessed by a bucket-type sub-model including three layers. The soil organic carbon (SOC) model derived from CENTURY (Parton et al., 1987), shares SOC out three major components, which include active (live and soil microbes plus microbial products), slow (resistant plant material) and passive (soil stabilized plant and microbial material) pools. Flows of carbon between pools are controlled by a decomposition rate and by a microbial respiration loss parameter, both depending on soil texture, soil moisture and temperature.

There are two main time steps in the model: half-hourly and daily. The simulation period typically ranges from days to years. Most of variables including fluxes (light penetration, photosynthesis, respiration, transpiration, rainfall interception) are simulated half-hourly; all the state variables (organ biomass, soil and carbon water content) and some other ones (growth and phenology) are simulated daily. Input meteorological driving variables, which can be either half-hourly or daily values, are global radiation, rainfall, wind speed, air humidity, air temperature and CO_2 air concentration.

A more comprehensive description of the model, including equations, is given in Dufrêne et al. (2005).

3. In situ measurements

3.1. Site characteristics

The experimental plot (Euroflux site FR02) is located in the State forest of Hesse (East of France; 48°40′N, 7°05′E) in a stand composed mainly of naturally established 30 years old beech trees (*Fagus sylvatica* L.). Three towers were erected: one (18 m high) is used for eddy covariance and microclimate measurements, the two other ones (15 m high) for physiological measurements. A hut containing the data acquisition systems is located near the first tower. A complete description of the site is given in Dufrêne et al. (2005) and Granier et al. (2000a).

3.2. Model parameterization data set

The majority of the input parameters (both climate and plant characteristics) are measured at the same experimental site (i.e. Hesse forest) as the validation data set. The parameter data set was measured independently of the validation data set (except rainfall interception parameters, which were calibrated). Finally, some parameters not available are taken from other beech sites and from literature. A complete description of the input parameters is given in Dufrêne et al. (2005).

Table 1
Light extinction coefficients (k) calculated using the simulated and measured profiles of PAR in the canopy

Julian day (1997)	Solar elevation (GMT) (h)	r^2	n	Measured k	Simulated k
217	14:56	0.74	45	0.63	0.66
223	8:41	0.55	73	0.69	0.72
223	10:07	0.43	73	0.65	0.61
223	11:46	0.66	73	0.64	0.61
232	12:47	0.80	75	0.67	0.66
232	14:45	0.68	78	0.59	0.66
Mean				0.65	0.65

Measurements were made for different days and solar elevations. We also provide the correlation coefficient (r^2) and the data size (n) of the relationship between the measurements and the fitted exponential.

3.3. Model validation data set

We used several independent data sets described below to evaluate the main sub-models. Most measurements were achieved during year 1997.

3.3.1. PAR profiles

At three dates in August 1997 and for different hours during the day (see Table 1), six vertical profiles of PAR were measured for different orientations around the scaffolding, using Li191-SA (Li-Cor, Lincoln, NE, USA) sensor. Profile of LAI were measured for the same orientations, using PCA-LAI2000 (Li-Cor) with three rings. To compare the measured and simulated profiles of PAR in a synthetic way, we have calculated the extinction coefficient (k) per date and per hour using Beer–Lambert law (Monsi and Saeki, 1953):

$$\frac{PAR}{PAR_{ref}} = \exp(-k \times LAI) \tag{1}$$

with PAR_{ref} the measured PAR on the top of the canopy.

3.3.2. Net radiation

A net radiometer (REBS, Seattle, USA) was installed above the stand at 17.5 m height, measuring the net radiation at 10 s time intervals and averaged and stored half-hourly. Some data (23 days) in winter were removed when daily temperatures are below 0 °C due to the frost on the net radiometer sensors (Granier personal communication).

3.3.3. Branch photosynthesis and night respiration

Two transparent branch bags were used to monitor the CO_2 exchange of branches during the 1997 growing season (end of April to early November).

One bag was placed near the top of the canopy (13 m above ground level, 0.4 point of LAI above, LMA = 92.0 g_{dm} m^{-2}) and a second one was placed at 7 m (4.8 point of LAI above, LMA = 41.8 g_{dm} m^{-2}). During measurements, bags were closed for 3 min and used as cuvettes operating as a closed system. Bags were scanned sequentially every half hour and monitored by a data logger. Between measurements, bags were supplied with ambient air (45 l s^{-1}). A similar system was described by Dufrêne et al. (1993) and used in the BOREAS project (Saugier et al., 1997). Net photosynthesis was calculated by subtracting woody branch respiration to net CO_2 exchange, and compared with simulated net photosynthesis for the considered layer. Branch respiration was calculated using a Q_{10} approach; parameters were measured monthly on branches outside the bag (Damesin et al., 2002, see below). Night foliage respiration was calculated and compared with simulation using the same approach.

To allow the comparison between measurements and model results at the branch level, some modifications were been made in the model. Firstly, the simulated PAR was lowered (−10%) to take into account plastic frame and walls reflectance, which reduces the amount of PAR inside the bag during the measurements (Dufrêne et al., 1993). Secondly, the simulated transpiration and growth respiration of leaves were, in this case, simulated per canopy layer.

3.3.4. Above ground wood respiration

CO_2 efflux were measured on stems at 1.30 m height, using temporary clamp-on chambers made of two half-cylinders of transparent, hard acrylic resin. During records, the air inside the chamber was homogenized by a fan. Between two consecutive

measurements, the chamber air was flushed with ambient air by increasing the fan speed for several minutes. Carbon dioxide efflux was measured on the airtight closed system using a solid-state IRGA gas analizer. Stem respiration measurements were conducted each month from March 1997 to February 1998 on 15 different trees pooled into five diameter classes.

Efflux of CO_2 from branches was also continuously measured at three levels in the crown, on one tree in 1997 and four trees in 1998. Branch respiration measurements were performed automatically in an open system, each cuvette being scanned sequentially during 5 min every 90 min and monitored by a data logger. Both systems were described and results were analyzed in Damesin et al. (2002) and Ceschia et al. (2002). In order to compare directly with the models predictions, these results were scaled up from local measurements to the ecosystem on a monthly basis separating maintenance and growth respirations (see Damesin et al., 2002 for more details about scaling up).

3.3.5. Soil autotrophic and heterotrophic respirations

Soil CO_2 efflux was measured using a portable closed respiration system (LiCor Inc., USA) as described in Epron et al. (1999a). Every two to four weeks, 12 measurements were recorded at randomly selected locations on each sub-plots during an 8-h period from 8a.m. to 4p.m. Six sub-plots of about 100 m² each were randomly chosen within the experimental plot for soil CO_2 efflux measurements. Two 3 m² sub-plots with no tree were created in June 1996 by digging around 1 m deep trench, lining the trench with a polyethylene film and filling it back with soil (see Epron et al., 1999b for a more comprehensive description). Daily means were calculated for both total (main plots) and heterotrophic (trenched plots) soil respirations allowing a comparison with model simulations.

3.3.6. Sap flow

The thermal dissipation technique (Granier, 1985, 1987) was used to measure sap flow over the growing season on 10 trees from codominant and dominant crown classes. Besides this experiment, two other preliminary experiments were previously undertaken. The first one was aimed at determining the radial variation of sap flux density within trunks in order to extrapolate to the whole trunk the sap flow measured in a 2 cm wide ring. A correction coefficient was then derived. A second experiment allowed relating sap flux density to tree circumference in order to scale sap flow from trees to stand (Granier and Bréda, 1996; Granier et al., 1999). Then, the transpiration rate established at the stand level is compared with model simulations.

3.3.7. Rainfall interception: throughfall and stem flow

Cumulative throughfall every seven days was measured using 42 raingauges disposed on a grid over the experimental plot. Throughfall was also measured automatically with two linear collectors, each one being collected with a tipping bucket raingauge and the data was recorded every 30 min (from day 176 to 241 in 1997). Stem flow was measured on seven trees from different circumference classes using spiral collecting rings disposed around the trunks and connected to tanks. Stemflow was measured weekly, hence cumulating one or several rain events, during the leafy period (i.e. six months) in 1997. A more complete description is given in Granier et al. (2000b).

3.3.8. Soil water content

During 1997, volumetric water content (θ) was measured weekly with a neutron probe (NEA, Ballerup, Denmark) in eight 160 cm deep aluminium access tubes. For comparison with model output, volumetric water content was summed for both top (0–30 cm) and deep (30–160 scm) soil layers.

3.3.9. The eddy covariance data set

The net exchange of both CO_2 and H_2O between the soil–forest ecosystem and the atmosphere was measured on the meteorological tower from January 1997 to December 1999 using the eddy correlation method (Leuning and Moncrieff, 1990). A complete description of the system used was given by Granier et al. (2000a). Profile of CO_2 between soil and top of the canopy was measured half-hourly allowing the calculation of CO_2 storage used to correct the net CO_2 fluxes (Fc). During 1997, the system works continuously. Measured half-hourly and daily data are directly comparable with total evapotranspiration (soil and canopy) and net ecosystem exchanges simulated by the model. For seasonal and annual comparison, missing data were gap filled using interpolation when

the gap is short (half-hour) or using empirical relationships for daily gaps according to Falge et al. (2001).

3.3.10. Annual water balance

Concerning the water balance, the soil evaporation (EP_{ground}) was not measured in Hesse, but Wilson et al. (2001) have estimated a mean value of 8% for the ratio soil evaporation above total evapotranspiration during the leafy period in a deciduous forest (Walker Branch Watershed) with a similar leaf area index ($L_{max} \sim 6\,m^2\,m^{-2}$). Using the fact that $ETR = Tr + EP_{ground} + IN$, we have estimated the soil evaporation in Hesse using the ratio EP_{ground}/ETR (0.08), the transpiration (Tr) and the net interception (IN) during the leafy period:

$$EP_{ground} = 0.08 \times \frac{Tr + IN}{1 - 0.08} \tag{2}$$

The transpiration is calculated from the sum of sapflow measurements during the leafy period and the interception is taken from Granier et al. (2000b). An estimation of the drainage (DR) was carried out during the leafy period using the following equation:

$$DR = P_i - IN - \Delta_{RW} - EP_{ground} - Tr \tag{3}$$

Δ_{RW} corresponds to the difference of soil water content between the beginning (May 2) and the end (October 27) of the leafy period used in Granier et al. (2000b) and P_i is the cumulated rainfall during the same period.

3.3.11. Annual carbon balance

Both CO_2 and H_2O fluxes, measured at different time steps, were summed over the year. Additionally, water fluxes were summed when leaf area index is maximum, from day 132 (May 12) to 259 (September 16). We used biomass increments estimated in 1997 for the stand by Le Goff and Ottorini (2001) and data from Bauhus and Bartsch (1996) for fine roots. Soil heterotrophic and autotrophic respirations were estimated by Epron et al. (2001). The maintenance leaf respiration was estimated using measured nocturnal respiration in branch bags. The woody branch respiration was subtracted from measurements (Damesin et al., 2002) and monthly coefficients for leaves (Q_{10} and basal respiration) were fitted across the data. Then, we applied these coefficients half-hourly over 24 h to calculate daily and finally, yearly leaf maintenance respiration. However, to allow a comparison with the model output, the level of respiration inhibition during daylight used in the model was also applied to daylight leaf measurements.

The gross primary production (GPP) is estimated by two methods: either by summing autotrophic respiration values ($R_{autotrophic}$) and measured biomass increments (Eq. (1)) or calculated from fluxes measured by eddy covariance (EC) as described in Granier et al. (2000a).

$$GPP = dB_{aerial\,wood} + dB_{coarse\,roots} + dB_{leaves}$$
$$+ dB_{fine\,roots} + R_{autotrophic} \tag{4}$$

In the same way, the ecosystem respiration ($R_{eco} = R_{heterotrophic} + R_{autotrophic}$) is calculated either by sum of each components of measured respiration or by estimation from EC measurements at a stand scale. The root respiration (needed in the first approach) is calculated as the difference between total soil respiration and heterotrophic respiration. The total annual soil respiration is set to the value of $663\,gC\,m^{-2}\,year^{-1}$ (Epron et al., 1999a,b) and a proportion of 52% of heterotrophic respiration in the total soil respiration is used (Epron et al., 2001). Foliage maintenance respiration was estimated from the branch bag measurements: monthly Q_{10} was derived from nocturnal measurements (only when no leaf growth occurs) and used to estimate a continuously foliage respiration assuming a daylight inhibition of 62% according to Villar et al., 1995. The growth respiration of leaves was not independently measured and we calculated it simply as the ratio of biomass increments estimated from LMA measurements and the construction cost for respiration (equal to 0.2, cf. Niinemets, 1999).

Finally, the annual net ecosystem exchange is calculated (i) as the difference between GPP and R_{eco} estimated by sum of fluxes, or (ii) directly summed using half-hourly eddy covariance (EC) measurements.

To compare the modelled NEE and the EC measurements, we also computed the sum of fluxes during different periods. We separated diurnal and nocturnal fluxes, leafy and unleafy season, with or without rain and before or after August 1 (beginning of edaphic drought).

4. Model simulations

We simulated all the processes either with mean values of input parameters or by taking into account an

uncertainty on 17 key input parameters. To determine the key input parameters, 150 sets of 1000 simulations were performed with a 10% Gaussian random noise on each of the 150 input parameters. An uncertainty analysis is then presented to evaluate the error on the annual outputs caused by uncertainties in these sensitive inputs parameters. Uncertainties on these parameters are estimated using in situ data. These uncertainties are used to create an ensemble of 17,000 simulations where the values of the 17 key parameters are randomly selected using Gaussian random distributions. The methodology of the uncertainty analysis and the key parameters are described in Dufrêne et al. (2005).

5. Results and discussion

5.1. Profile of PAR

The extinction coefficients, calculated using the profile of PAR simulated by the model, appear very close to the measured values (Table 1). However, the correlation coefficient between the fitted exponential curves and the measurements, is not always high (r^2 ranging from 0.43 to 0.80) and the measured PAR extinction often decreases at a higher rate than the fitted exponential relationships (data not shown).

5.2. Global net radiation

As shown in Fig. 1, we observe a very close relationship between daily simulated and daily measured global net radiation values (Rn) ($y = 1.05x - 1.13$, $r^2 = 0.97$). Nevertheless, during leafless period, the model sligthly underestimates the low values of global net radiation.

5.3. Branch photosynthesis, transpiration and night respiration

Considering the branch bag at the top of the canopy, the model captures well the seasonal pattern and the short term variation of daily net photosynthesis (Fig. 2a, $y = 0.87x + 0.54$, $r^2 = 0.78$, d.f.[1] = 158) showing an underestimation during the leaf growing phase (until end
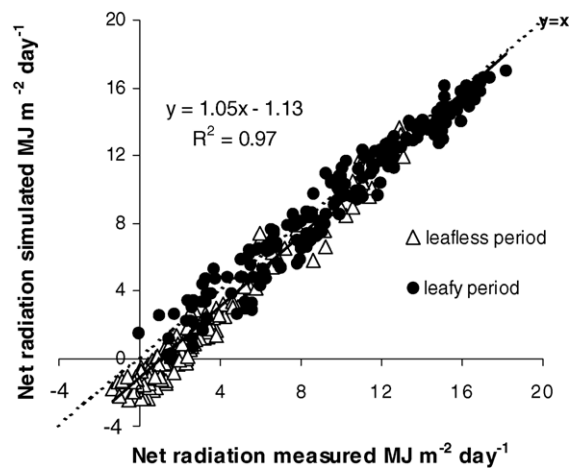
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[1] d.f.: degree of freedom, i.e. number of points considered in the regression calculation.

Fig. 1. Simulated vs. measured daily net radiation (MJ m^{-2}) during 1997. Results are separated between leafy period ($\bullet$) and leafless period ($\triangle$).

of May) and an overestimation starting in July and sensitive mainly during September and October. We found a good relationship between simulated and measured tree transpiration (Fig. 2c, $y = 1.36x - 0.01$, $r^2 = 0.89$, d.f. = 158) with overestimations, except an underestimation during the water stress period.

With the aim to test if a decrease in photosynthetic capacity during the year could explain the increasing overestimation in net photosynthesis by the model, we introduced a seasonal change in nitrogen content measured on sun leaves of mature beech trees in Orsay (data not published, $[N] = 0.191D_l - 0.464$, $r^2 = 0.89$, d.f. = 16, with D_l the daylight duration in hour and $[N]$ in %). Results presented in Fig. 2 (dotted lines) show a clear improvement of pattern in simulated net photosynthesis during the second part of the season (r^2 increases from 0.78 to 0.85) without significant change in transpiration rate. Moreover, simulated nocturnal foliage respiration is largely improved at the end of the season, when nitrogen dynamic is considered (Fig. 2b). Despite the fact that changes in nitrogen content were measured in a different place and a different year, introduction of this empirical relationship improves the model predictions. As the simultaneous decrease in nitrogen content and photosynthetic capacity during the year has been described by different authors for deciduous trees (Wilson et al., 2000; Frak et al., 2002), we can assume that this phenomenon occurred in Hesse during 1997.
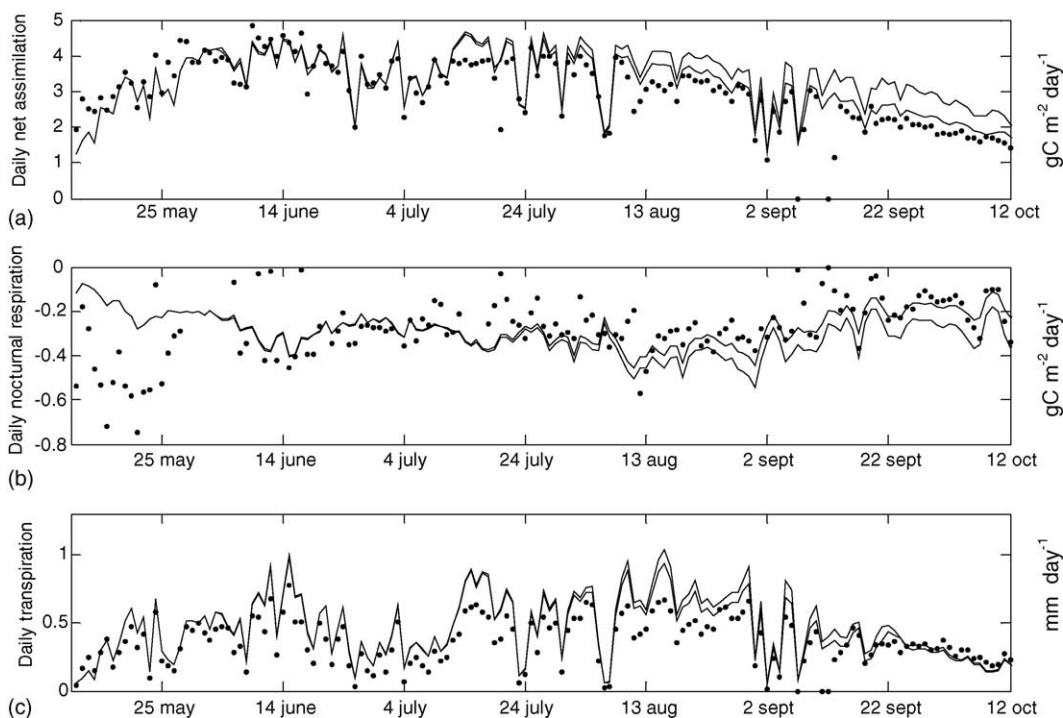
Fig. 2. Comparison between daily measurements (●) and simulations in upper branch bag (with constant nitrogen in solid line and variable nitrogen in dotted line). (a) Daily net assimilation in $gC\,m^{-2}\,day^{-1}$; (b) nocturnal respiration of leaves in $gC\,m^{-2}\,day^{-1}$; (c) transpiration of leaves in $mm\,day^{-1}$.

Considering "the lower branch bag", both net photosynthesis and transpiration are largely underestimated by the model (Fig. 3a). Using measured PAR and LMA inside the bag rather than simulated PAR and LMA, reduces in a large extent the discrepancy between model and measure, but an underestimation persists. With the aim to understand this remaining difference, we tested the possible effects on net photosynthesis of an increase from top to bottom in the canopy of (i) measured leaf nitrogen content, and (ii) leaf absorbance (according to increase in amount of chlorophyll and leaf mass per leaf area). Both are generally observed in the deciduous canopies (Niinemets, 1995; Niinemets and Tenhunen, 1997) but not considered in the model CASTANEA. However, these effects cannot explain the low simulated photosynthesis.

The simulated nocturnal foliage respiration is largely overestimated all along the leafy period except very early and very late in the season (Fig. 3b). This overestimation could be due to errors in

estimating branch respiration inside the bag or to an overestimation of shade leaves respiration by the model.

According to the large observed heterogeneity in the light level at the base of the canopy, we can conclude that the simulated PAR, which is an average value within the considered layer, is not representative of the local branch bag condition. This is probably the main cause for net photosynthesis differences between observed and simulated values. The simulated transpiration is also underestimated in "the lower branch bag" and this corroborates the conclusion founded with photosynthesis simulations: as for the PAR, the average global radiation budget is probably not representative of the local branch bag condition.

5.4. Aerial wood respiration

Daily maintenance branch (Rbr) and stem (Rst) simulated respirations are very similar to the
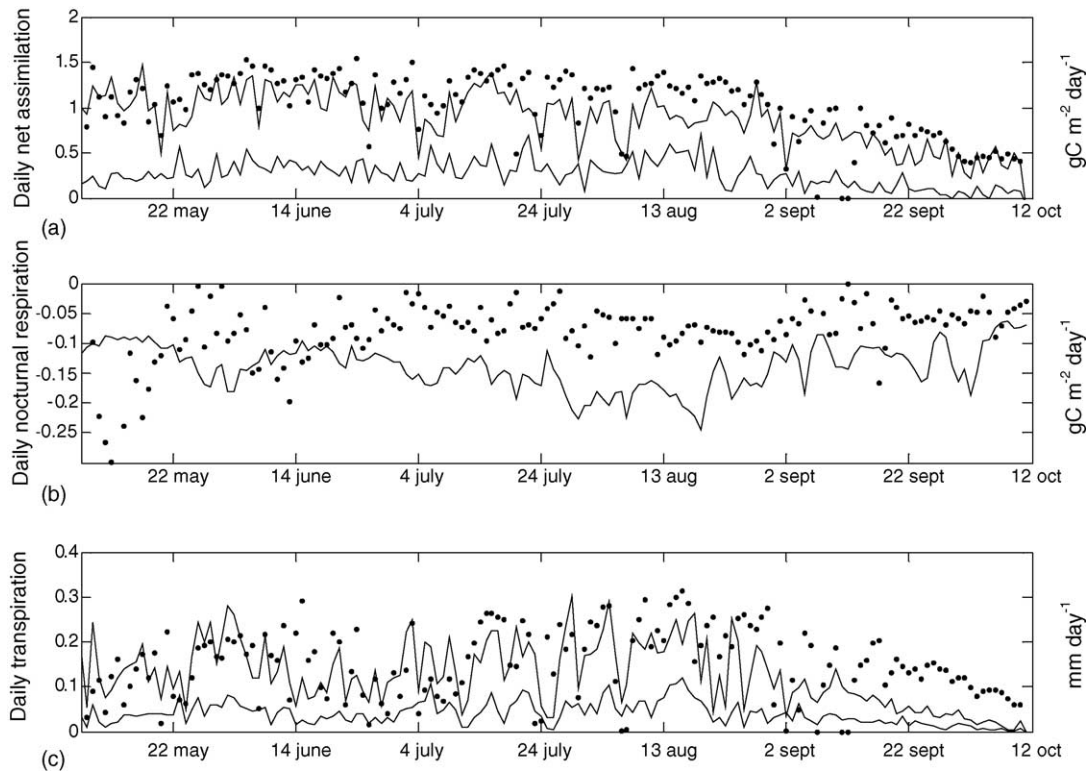
Fig. 3. Comparison between daily measurements (●) and simulations (with simulated PAR in solid line and forcing with measured PAR in dotted line) in lower branch bag. (a) Daily net assimilation in $gC\,m^{-2}\,day^{-1}$; (b) leaf nocturnal respiration in $gC\,m^{-2}\,day^{-1}$; (c) leaf transpiration in $mm\,day^{-1}$.

those derived from measurements ($Rbr_{simulated} = 0.90Rbr_{measured} + 0.01$, $r^2 = 0.997$; $Rst_{simulated} = 0.96Rst_{measured} + 0.02$, $r^2 = 0.991$). The model used constant Q_{10} and basal respiration parameters on an annual basis for each organ in opposition to the field data were monthly measured parameters were used. Consequently, we can conclude that seasonal (i.e. monthly) changes in those parameters have a negligible influence on both daily (data not shown) and yearly (see Table 2) maintenance respiration of aerial woody organs.

5.5. Soil autotrophic and heterotrophic respiration

Simulated heterotrophic soil respiration has already been tested by Epron et al. (2001). However, according to slight changes in model parameterization and also considering the interdependence of several

processes in the model (e.g. when photosynthesis rate changes, growth of roots and consequently root growth respiration change without changing allocation coefficients), we examine both microbial heterotrophic respiration and total soil respiration (i.e. heterotrophic + autotrophic). Simulated heterotrophic soil respiration is very similar to the previous version of the model and compares well with measurements (see Fig. 1a in Epron et al., 2001). Total simulated soil respiration is presented in Fig. 4, showing a good agreement with measured values except from mid-June to mid-August when simulated values are largely underestimated. This underestimation is largely due to low simulated values of autotrophic root respiration. One hypothesis could be an underestimation of the fine root biomass or of the fine roots growth during the summer, both controlling the fine root respiration. The fine root biomass could be misestimated from

Table 2
Comparison between annual simulated (with or without uncertainties on 17 key input parameters) and measured carbon fluxes and biomass increment (in $gC\,m^{-2}\,year^{-1}$) with two different approaches: sum of separated fluxes and integrated flux by eddy covariance measurements (Granier et al., 2000a)

Variable	Simulated without uncertainties	Simulated with uncertainties	Integrated measured flux	Separated measured fluxes	Methods concerning the measurements of separated fluxes	Sources
Sum of separated fluxes						
Biomass increment (aerial wood)	363	347 ± 48		379	Dendrometric measurements	Le Goff and Ottorini (2001)
Biomass increment (coarse roots)	84	80 ± 10		76	Root system excavations	Le Goff and Ottorini (2001)
Biomass increment (leaves)	175	175 ± 19		131	Litter collection	Granier et al. (2000a)
Biomass increment (fine roots)	172	166 ± 27		171		Bauhus and Bartsch (1996)
Increment of carbo-hydrate storage	−8	−29 ± 37		–	Included above (see text)	
Rroots	220	215 ± 17		325	By difference (see text)	Epron et al. (2001)
Rm stems	89	89 ± 17		77	Chambers	Damesin et al. (2002)
Rm branches	82	83 ± 13		75	Chambers	Damesin et al. (2002)
Rc wood	138	131 ± 24		130	Chambers	Damesin et al. (2002)
Rm leaves	171	170 ± 31		168	Branch bags	This study
Rc leaves	35	35 ± 20		26	Calculated	
GPP	1518	1456 ± 151	1245	1558	Sum of fluxes	
Rheterotrophic	321	321 ± 5		338	Trenched plots	Epron et al. (2001)
Reco	1057	1044 ± 75	988	1139	Sum of fluxes	
NEE	463	413 ± 119	257	419	Sum of fluxes	

mid-June to mid-August, if carbon allocation to roots or fine roots turnover vary during the season while the used version of the model assumes constant allocation coefficients and turnover from budburst to leaf fall.
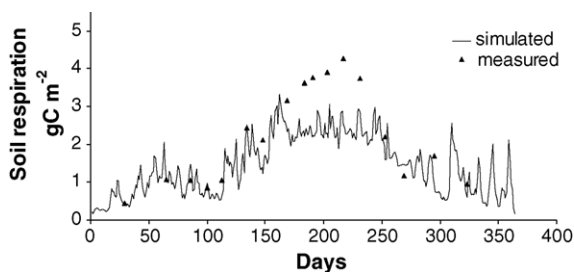

Fig. 4. Simulated and measured daily soil respiration (heterotrophic + root autotrophic) in Hesse during 1997.

5.6. Net ecosystem carbon exchange (NEE)

5.6.1. Half-hourly time scale

In the half-hourly time scale analysis, we voluntarily excluded winter and September dry periods (see daily time scale and seasonal pattern below); all the results correspond to a period comprised between May and end of August. During this period, the model captures well the daily pattern of NEE as shown on the few days during June in Fig. 5a. Simulations do not reproduce the high variability of nocturnal fluxes. From May to September simulations are closed to measurements (Fig. 5b). Nevertheless, we note a better fit when we consider data averaged over 3 h rather than half-hourly data (half-hourly: $NEE_{sim} = 0.76 NEE_{mes} + 1.65$, $r^2 = 0.72$; 3-h: $NEE_{sim} = 0.90 NEE_{mes} - 1.12$, $r^2 = 0.86$). We can
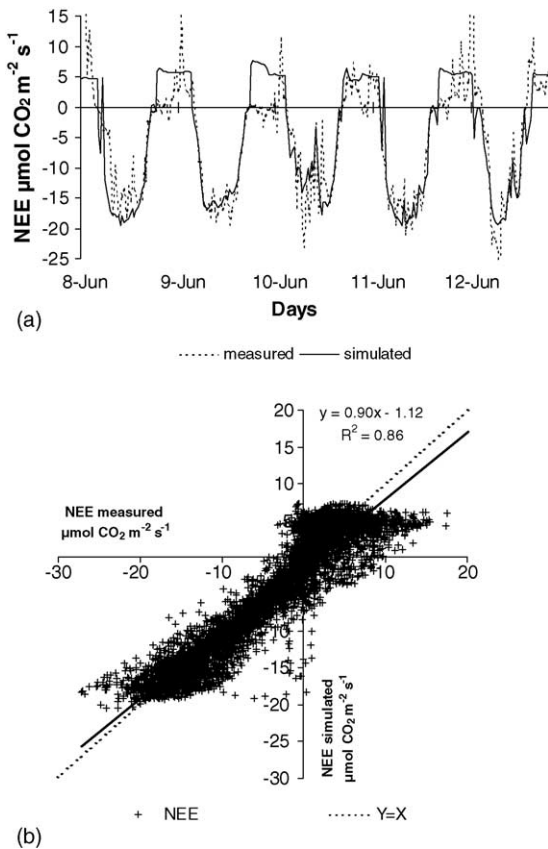
Fig. 5. Measured and simulated half hourly NEE (μmol CO_2 m^{-2} s^{-1}) in Hesse in 1997. (a) Daily pattern of simulated and measured NEE, from May 23 to May 27; (b) comparison of measured and simulated half hourly NEE averaged over 3 h during 1997. Linear regression and the straight line $y = x$ are also plotted.

conclude that the model is not able to capture properly all the short-term (half-hourly) NEE variations, especially at night.

5.6.2. Daily time scale and seasonal pattern

During the winter period, the total "ecosystem respiration" (coarse and fine root + soil heterotrophic) was estimated accurately by the model including the autumnal respiration peak (Fig. 6a). The length of the growing season was well reproduced and despite the simple hypothesis assuming a constant leaf nitrogen content over the season, the seasonal pattern of NEE is properly captured (Fig. 6a). During all the leafy period, we note a trend to overestimate the lowest daily NEE values and to underestimate the highest ones.

From early September to the end of the leafy period (end of October) simulated NEE are systematically overestimated.

By introducing a seasonal decrease in leaf nitrogen content (same way as in a Branch Bag) we do not improve strongly the accuracy of the model prediction ($r^2 = 0.81$ instead of 0.79) and contrary to the Branch Bag, simulated NEE remains overestimated in September and October. During this period, the predicted soil water content was above measured values (see Fig. 8c) and this led to an overestimation of photosynthesis and consequently of NEE. By forcing the measured soil water content we tested that this underestimation of the water stress could explain all the differences between the simulated daily NEE and the measured one between the September 18 and the October 9 but this was not the case later in the season.

If we consider NEE only during the daylight period (Fig. 6b) then predictions are improved ($r^2 = 0.87$; less scatter) except during September dry period (large overestimation). This is due to a better prediction of daylight fluxes compared with night fluxes, except during the dry period when night respiration was overestimated (Fig. 6c), partly compensating for the assimilation overestimation. During the leafy period, the day to day variability of the nocturnal NEE is much higher than during the leafless period. Like in the case of the half-hourly time step, the model is not able to reproduce this large variability observed between nights.

5.7. Transpiration, evapotranspiration and soil water balance

5.7.1. Half-hourly time scale

As for the NEE, in the half-hourly time scale analysis, the results correspond to the period comprised between May and the end of August. Simulated transpiration rates compare well with sapflow measurements ($TR_{sim} = 0.92 TR_{mes} + 0.15$, $r^2 = 0.88$). By introducing a time lag of one half-hour to take into account the stem water buffer, the relationship was slightly improved (r^2 increases from 0.88 to 0.90 without any significant change in slope and intercept). A time lag between sapflow and canopy transpiration (directly measured or estimated by a model) has often been reported (Granier et al., 2000b) and is observed here again (Fig. 7a). Furthermore, we note only a slight improvement, considering data averaged over 3 h rather than half-hourly data

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(r^2 increases from 0.88 to 0.93, Fig. 7b). We can conclude that the model is more able to capture properly the short-term (half-hourly) TR variation measured using sapflow than NEE variation measured using the eddy-covariance technique.

The relationship between simulated and measured evapotranspiration is much more scattered (data not shown) than the transpiration one ($ETR_{sim} = 0.74 ETR_{mes} + 0.99$, $r^2 = 0.61$, d.f. = 5952). The relationship was improved when only considering
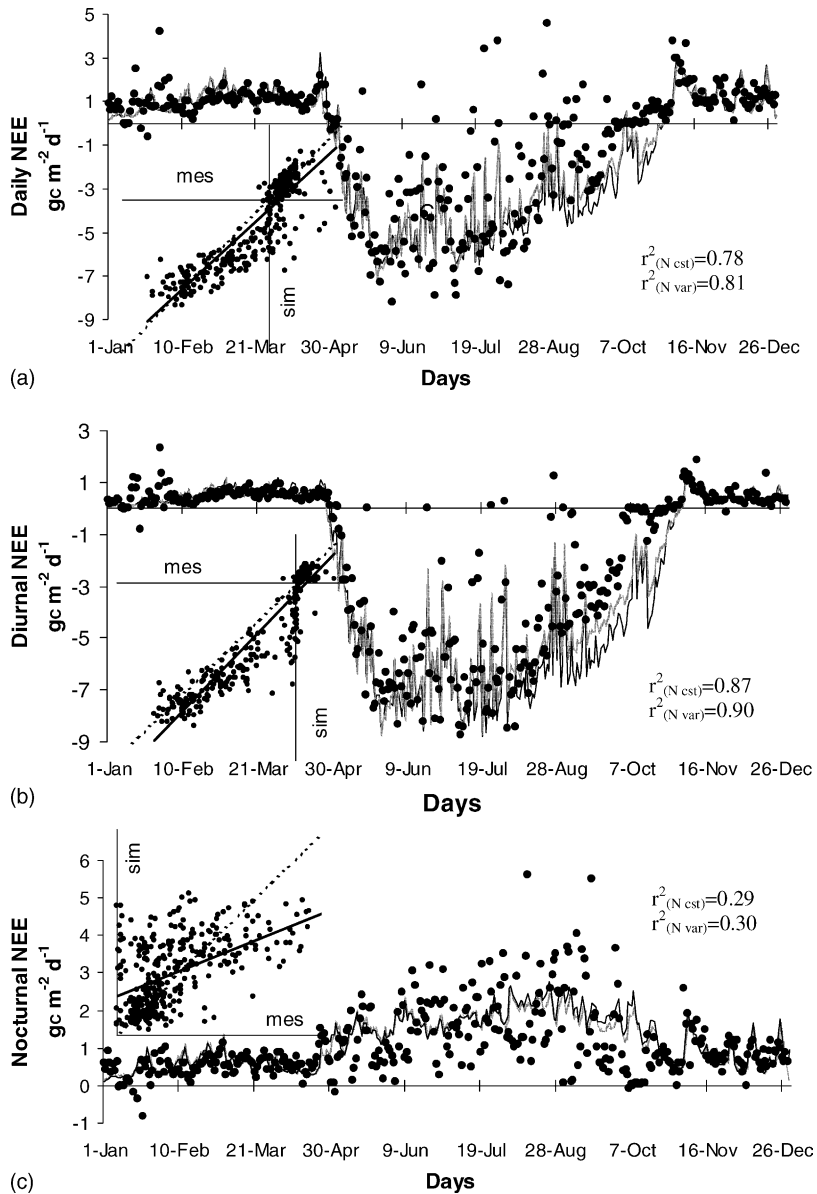

Fig. 6. Temporal dynamic of daily NEE in $gC\,m^{-2}\,day^{-1}$ (measured in black circle and simulated in solid line) for constant nitrogen (N_{cst}) and grey line for variable nitrogen (N_{var}). (a) Sum over the entire day (Daily NEE); (b) Sum over the diurnal period (Diurnal NEE); (c) Sum over the nocturnal period (nocturnal NEE). Results for N_{cst} are also plotted as measured vs. simulated.
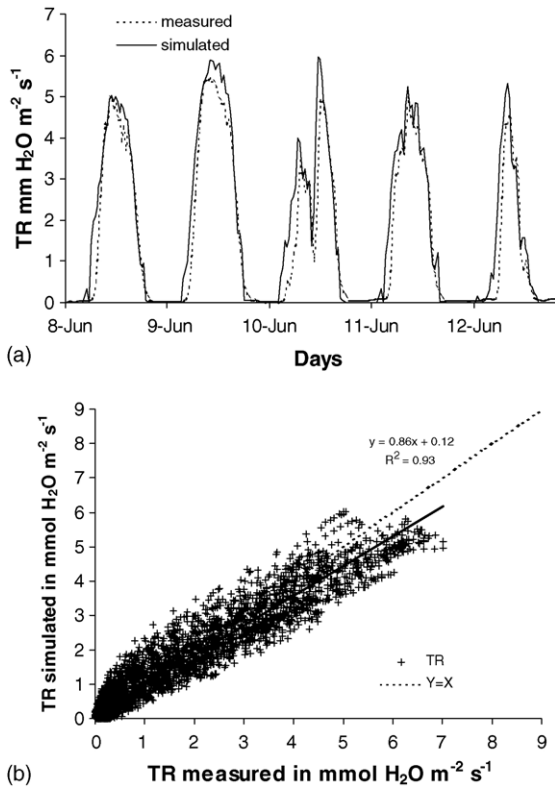
Fig. 7. Half-hourly transpiration (TR mmol H_2O m^{-2} s^{-1}) measured and simulated in Hesse during 1997. (a) Daily pattern of simulated and measured TR, from May 23 to May 27; (b) comparison of measured and simulated half hourly TR during 1997 without time lag. Linear regression and the straight-line $y = x$ are also plotted.

periods without rain ($ETR_{sim} = 0.75ETR_{mes} + 0.85$, $r^2 = 0.67$, d.f. = 2689).

5.7.2. Daily time scale and seasonal pattern

If we consider only days without rainfall, CAS-TANEA reproduces properly the total daily evapotranspiration (Fig. 8a) during the winter and during the growing season as well ($ETR_{sim} = 1.04ETR_{mes} + 0.25$, $r^2 = 0.87$, d.f. = 324). However, we note a tendency to overestimate the lowest daily values even during periods without water stress (i.e. from mid May to end of July). For rainy days, model largely overestimates measured values (data not shown) all along the year ($ETR_{sim} = 0.95ETR_{mes} + 1.09$, $r^2 = 0.43$, d.f. = 174). We can assume that the model overestimates evaporation during these days, because the simulated transpiration is well correlated with measured sapflow (Fig. 8b, $TR_{sim} = 1.00TR_{mes} - 0.01$, $r^2 = 0.93$, d.f. = 185), even during rainy days. Energy reaching the soil during the leafy period is generally less then 5% of the incident energy in the Hesse forest because of high LAI values and of planophile leaf angle distribution. Consequently, the soil evaporation is low and the model reproduces these low values (less then 0.6 mm day^{-1} in average). In consequence we can assume that most differences between observed and measured evapotranspiration come from the part of rainfall, which is intercepted and re-evaporated by the canopy. If we now compare measured and simulated net interception of rainfall during the leafy period, we find very similar values (Table 3), which is not surprising if we consider that rainfall interception parameters were partly calibrated using the same data set (Dufrêne et al., 2005). Moreover, the model simulates properly or even overestimates the available soil water content, whereas the contrary would have occurred if net interception, canopy evaporation or soil evaporation were systematically overestimated. According to the observations mentioned above, we believe that the model reproduces properly wood and canopy interception and evaporation. On the other hand, we can conclude that (i) eddy-covariance measurements underestimate water vapor fluxes during rainy events (Granier et al., 2000b, 2003), and (ii) the model overestimates the lowest values of daily evapotranspiration.

Table 3
Comparison between simulated and measured water fluxes (in mm year^{-1}) during the leafy period (from May 2 to October 27)

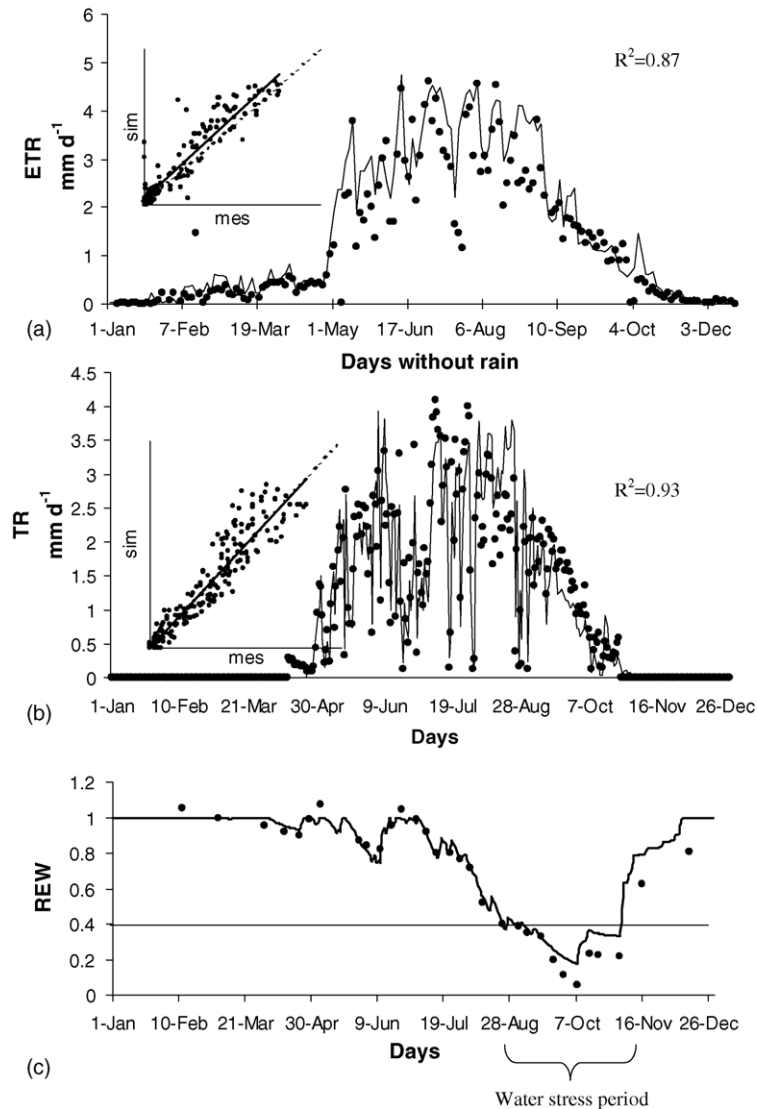| Variable	Simulated	Measured	Method	Sources
Transpiration	316	310	Sapflow	This study
Net interception	111	125	Raingauges under canopy	Granier et al. (2000b)
Soil evaporation	59	38	Calculation (see text)	
Evapotranspiration	486	317	Eddy covariance	Granier et al. (2000b)
Drainage	64	89	Calculation (see text)	
Rainfall	438	438	Raingauge above canopy	

Fig. 8. Temporal dynamic of daily water fluxes measured and simulated. (a) Evapotranspiration (ETR) in mm day^{-1} only for days without rain; (b) transpiration (TR) in mm day^{-1}; (c) relative extractable water (REW) in the soil. For (a) and (b), results are also plotted as measured vs. simulated.

As mentioned above, the model reproduces accurately the soil water content evolution until end of August, but when the soil water stress increases it provides overestimated values (Fig. 8c). The transpiration simulated during the discrepancy period (i.e. September 23 until October 9) is close to that measured by the sapflow technique (Fig. 8b) with a tendency to underestimate (cumulated deficit is 8 mm). During this period no rain occurred, thus there was no water evaporated from

rainfall interception. In consequence this difference between predictions and measurements can only result from an underestimation of the simulated drainage.

5.7.3. Water use efficiency

While drought effects on assimilation have been extensively studied at the leaf level, few attempts have been made to test the assumption concerning the way to take into account these effects at the
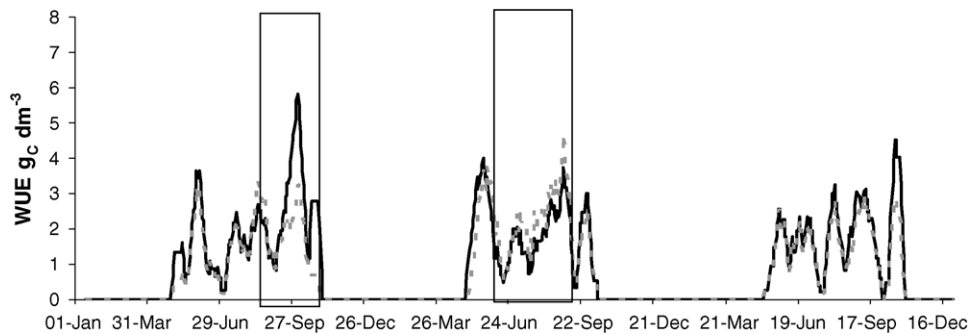
Fig. 9. Temporal dynamic of daily water use efficiency (GPP/TR) derived from eddy covariance and sapflow measurements (grey dashed line) and simulated by CASTANEA (in solid black line). Results are sliding average over 14 days. The water stress period is represented in grey and defined as the days when the soil relative extratable water (REW) is below 0.4.

stand level (Reichstein et al., 2002). In *Quercus ilex* ecosystems, Reichstein et al. (2002), demonstrated that the approach of Sala et al. (1996) for including water stress effects lead to discrepancies in water use efficiency, in fluxes and in annual balances. The exact result also depends on the process of parameterization (Reichstein et al., 2003).

We have tested the way of including the effects of water stress on assimilation in the Hesse site for three contrasted years. For that aim, the water use efficiency (WUE) was estimated from the ratio between daily GPP (eddy covariance estimate) and daily transpiration (sapflow estimate) from 1997 to 1999. In 1997, the drought occured very late in the season, while in 1998 it occured in the middle of the season. There was no water stress in 1999. In 1998 and 1999 the seasonal evolution of WUE is well described by the model (Fig. 9). But in 1997, while the drought occurs very later in the season, the model simulates a too pronounced increase of WUE from end of August. Consequently, for this species when the water stress is moderate or occurs early, the model of Sala et al. (1996) allows an accurate simulation of the WUE dynamics. But when drought and leaf ageing occur simultaneously, which is not common in European oceanic climate, a strong decrease in photosynthetic capacities should probably also be taken into account.

5.8. Annual carbon and water balances

5.8.1. Water balance

The annual simulated transpiration (311 mm) is close to that derived from sapflow measurements

(313 mm). By contrast, the total evapotranspiration is much higher in the model (596 mm) than that measured by EC (351 mm). As explained above (in the daily pattern of evapotranspiration) this difference mainly occurs during rainy days. There is probably an underestimation of measured evapotranspiration by the EC when canopy is wet. This hypothesis is confirmed by the analysis of the annual water balance during the leafy period (Table 3). The sum of measured interception, soil evaporation and transpiration (473 mm) is close to the value given by the model for total evapotranspiration (489 mm), and strongly differs from the value measured by EC (317 mm).

We also note that the model tends to underestimate the drainage (64 mm instead of 89 mm). Granier et al. (1999) have reported that several field experiments have shown that important drainage could occur in the lower soil layers even in dry soils. This could explain our underestimation of both drainage and soil water deficit at the end of the leafy season.

5.8.2. Carbon balance

Simulated and measured (or estimated from measurements) values are presented in Table 2. We calculated the annual net ecosystem exchange using two methods: Firstly, we estimated the annual carbon balance by summing all individual fluxes. Secondly, NEE was measured by the eddy covariance technique, and R_{eco} and GPP were calculated using both eddy covariance measurements and Q_{10} based relationship (Granier et al., 2000a).

Note that, concerning leaf growth respiration, the model uses a construction cost for leaf growth

respiration established from local measurements and so we cannot compare measurements and simulations, which are not independent. However, the model validation for total respiration is not concerned since leaf growth respiration corresponds only to 3% of the total annual respiration.

The model provides an accurate estimation of all respiration and biomass increments, independently measured except for root respiration, which is underestimated. Consequently, R_{eco} calculated (from measurements) using the first method is above the modeled one (+7%). The annual measured GPP is also slightly higher (+2.5%) than the simulated one, and as a result the model overestimates the net ecosystem exchange of 44 gC (i.e. +10%). To conclude, we note that a precise estimation of NEE requires that the model accurately reproduces both GPP and R_{eco}: in our case a small difference in root respiration causes a strong difference in NEE. For these reasons, the belowground allocation and respiration require more measurements and modeling works. The bias caused by assuming that the input model parameters are spatially constant (cf. Dufrêne et al., 2005), cannot be an alternative explanation of the difference observed between the modeled NEE and the NEE measured by the sum of fluxes approach (Table 2).

We can also observe that GPP, R_{eco} and NEE estimated by summing CO_2 fluxes from the different compartments differ strongly from those estimated by EC measurements (respectively, 25%, 15% and 63%). Granier et al. (2000a) had the same conclusion, even if the difference was smaller (for GPP: 13%, instead of 25% in our calculation). According to the differences between the two approaches for estimating GPP, R_{eco} and NEE from measurements and the good agreement between simulated values and the first approach estimation, the model prediction shows large differences with EC measurements (respectively, 22%, 4% and 80% for GPP, R_{eco} and NEE).

It is not surprising that the model gives results closer to the first measurement method, even if the sub-models were not calibrated but parameterized using independent data sets because the way to scale-up from local measurements (or simulations) to stand estimation (or simulation) is very similar. Moreover, the model parameters were measured at similar scales as the measurements of local fluxes used for validation.

It is necessary to consider different potential sources of errors to understand the large discrepancies between the results from the two approaches using measurements (i.e. scaling local fluxes from each process and integrative EC data).

Firstly, the respiration of the dead woody organs (mainly branches remaining on the soil after thinning) is not taken into account in the model and in the "summed-fluxes" approaches, whereas this respiration is incorporated in the integrated fluxes (EC). This could explain, at least partly, the difference in NEE (Table 2).

Secondly, in order to estimate the R_{eco} from EC measurements, we summed the night ecosystem respiration measurements and the daily ecosystem respiration. Daily ecosystem respiration is calculated from a Q_{10} relationship established between night respiration measurements and air temperature and applied during the day using diurnal temperatures. The daily respiration calculated in this way could be underestimated, which could explain the difference in R_{eco} (Table 2).

Nevertheless, these two hypotheses are conflicting. An increase of the R_{eco} by taking into account dead wood in the sum of fluxes approach, leads to amplify the discrepancy with the EC estimations. On the other hand, during the leafless period the simulated fluxes are closer to the EC measurements (Table 4).

As the model gives results close to the sum of fluxes approach, it allows to test some hypotheses to explain the differences with the EC measurements. The diurnal fluxes during the leafy period correspond to the difference between GPP and diurnal R_{eco}. A comparison of measured (EC) and modeled diurnal fluxes is presented in the Table 4 by separating the days with or without rain and the days before or after the drought period. The model overestimates the diurnal fluxes, essentially for rainy days and after the August 1. Before the drought the model slightly overestimates the diurnal fluxes of 10% for days without rain and 19% for the others. During and after the drought the overestimation becomes 53 and 139%. The rainy effect is maybe due to an underestimation of CO_2 fluxes by EC during rainy events (as for the evapotranspiration) and can partly explain the differences between the two approaches.

Concerning the seasonal effect, the overestimation of diurnal modeled NEE during the drought was already discussed for daily results. However, it is necessary to understand why, despite this overestimation, the modeled GPP is close to the estimation made by

Table 4

Comparison between annual NEE fluxes (gC m^{-2} per year), simulated and measured by EC techniques

NEE	Simulated	Measured	Variation in %
Diurnal leafy without rain before the August 1	253	230	+10
Diurnal leafy with rain before the August 1	311	261	+19
Diurnal leafy without rain after the August 1	282	184	+53
Diurnal leafy with rain after the August 1	149	62	+139
Nocturnal leafy	−340	−296	+15
Diurnal leafy	994	737	+35
Leafy	644	441	+46
Leafless	−181	−178	−2

We separated diurnal and nocturnal, leafy and leafless, with and without rain, before and after the August 1 (drought period).

the sum of fluxes approach. It is thus possible that the drought had a greater effect on EC fluxes than on the local fluxes. To explain this, an interesting hypothesis concerns a possible scale effect with different forest areas generating different CO_2 fluxes. The area considered to measure model parameters and local fluxes (used to scale up) is different from the area concerned by EC measurements (Goulden et al., 1996). Moreover, the forest area concerned by EC measurements (i.e. footprint) changes according to wind direction and intensity. In particular, night flux came from a different area than daily fluxes and then estimating daily respiration using night measurements could lead to some bias. To test this hypothesis, coupling footprint of EC-fluxes and carbon fluxes models parameterized spatially appears to be a promising approach.

6. Conclusion

CASTANEA, a biophysical model, was applied to estimate stocks and fluxes of both carbon and water over a deciduous forest from hourly to annual time scales. The simulations were compared to measurements made at different spatial scales. The model reproduced quite well all the measured individual processes, except the root respiration, which was underestimated during summer. However, discrepancies with EC measurements were observed. Concerning evapotranspiration, error on EC measurements during rainy days could explain the difference between modeled and measured values. On the contrary, regarding CO_2, the reasons for discrepancies between the sum of local measurements and simulations, on one hand and EC measurements, on the other hand, remains to be clarified. However,

the scale effects of measurements and simulations, appear to be a good explanation and should be further studied.

We have also underlined the need of a very accurate estimation of each of the individual processes to accurately assess the resultant (i.e. the net ecosystem exchange). Some important processes concerning carbohydrate allocation or fine roots turnover were not measured and consequently not directly tested (only indirectly using respiration). We can conclude that more effort should be made on studying and modeling both root respiration and root turnover.

The fact that the model was validated for most of the individual processes, which is generally not the case, lead us to have confidence in its general validity and applicability on other sites and species, where similar studies are currently undertaken. These new tests and validations should also include long-term fluxes and growth data.

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