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Effect of aggregating spatial parameters on modelling forest carbon and water fluxes

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Abstract

Estimating spatial variability of carbon and water fluxes is an essential task in ecological modelling. In this article, the sensitivity of carbon and water fluxes to the spatial variability of biochemical and structural properties of canopies is assessed in beech forests using a process-based model (CASTANEA). Firstly, a sensitivity analysis was carried out by varying simultaneously a combination of six key parameters within a realistic range: the above ground wood biomass (B), the soil water reserve (S_{WR}), the canopy clumping factor (C_F), the leaf area index (L), the leaf mass per area of sunlit leaves (M_{sun}) and the leaf nitrogen content (N). Secondly, three spatial scales of variability were considered using three study sites whose areas ranged from 0.8 to 1000 ha. The first area studied was a heterogeneous stand located in old-growth forest in Fontainebleau (south of Paris, France). The spatial variability of the biophysical and biochemical ecosystem characteristics in 80 m² out of 100 m² was determined. For the two other case studies, we selected a sample of nine plots in which the key input parameters were measured. Sensitivity analysis indicated that photosynthesis and ecosystem respiration show a moderate non-linear response to L, S_{WR} and B. In spite of these non-linear responses, the three case studies revealed that using parameters averaged over the whole area, induces only a slight bias in the estimation of carbon fluxes and almost no bias in the estimation of water fluxes. The implication of the low sensitivity of carbon and water fluxes to parameter aggregation is discussed in relation to the general problem of the scaling up fluxes from ecosystems to large forest regions. © 2006 Elsevier B.V. All rights reserved.

Keywords: Deciduous forest; Carbon balance; Simulation models; Spatial scale; Parameter averaging

1. Introduction

Carbon and water fluxes are controlled by a combination of several biophysical processes (photosynthesis, respiration, transpiration, evaporation, drai-

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nage, etc.), which generally occur at high spatial and temporal resolutions: from seconds to hours and from micrometers (organelle and microbe) to square meters (organ, plant and soil profile). In order to scale carbon and water fluxes up to higher spatial and temporal scales, each process should first be properly scaled. Because these processes do not respond linearly to the biochemical and structural properties of ecosystems, assessment of the spatial variability of ecosystem characteristics is an essential first step for ecological modelling. The use of an

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Nomenclature

В	Above ground wood biomass $(kg(C) m^{-2})$				
C_{-}	canopy clumping factor				
	aross primary production $(q(C))$ m ⁻²				
ULL	$year^{-1}$				
$H_{\rm soil}$	soil depth (mm)				
$k_{\rm LMA}$	Exponential coefficient of $M_{\rm L}$ decrease				
L	true leaf area index $(m_{leaves}^2 m_{soil}^{-2})$				
$L_{\ln av}$	equivalent leaf area index $(m_{leaves}^2 m_{soil}^{-2})$				
M _{sup}	leaf mass per area of sunlit leaves				
sun	$(g(DM) m^{-2})$				
Mт	leaf mass per area per leaf laver				
L	$(g(DM) m^{-2})$				
N	leaf nitrogen content $(g(N) g(DM)^{-1})$				
N	leaf nitrogen per unit leaf area				
¹ a	$(q(N) m^{-2})$				
NEP	$(g(\Gamma)) m_{leaf}$				
I LI	(g(c)) in productivity $(g(c))$ in $(g(c))$ in				
Þ	gan fraction				
I DEW	relative extractable water				
	relative extractable water acconstant respiration $(q(\mathbf{C}) m^{-2} vor^{-1})$				
R _{eco}	betarotrophia respiration $(g(C) \text{ in } year)$				
Λ _h	(g(C)) in $(g(C))$ in $(g(C))$ in				
C	year)				
S_{WR}	soll water reserve (mm)				
	transpiration (mm)				
V _{cmax}	maximal carboxylation rate (μ mol(CO ₂) m ⁻² s ⁻¹)				
V_{jmax}	potential rate of electron flow				
0	$(\mu mol(CO_2) m^{-2} s^{-1})$				
Greek le	etters				
$\sigma_{ m base}$	standard deviation obtained when all				
	input parameters are variable together				
$\sigma_{ m sum}$	sum of the standard deviations, obtained				
	when input parameters are variable one				
	by one				
ω_j	azimuth angle for hemispherical photo-				
	graphs (radian)				
θ_i	zenith angle for hemispherical photo-				
	graphs (radian)				
$\theta_{\rm fc}$	soil water content at the field capacity				

 $(m^{-3}(H_2O) m_{soil}^{-3})$ θ_{wilt} soil water content at the wilting point

arithmetic average of a spatially variable parameter could be inappropriate when processes exhibit strong nonlinear responses to this parameter. This can lead to a significant bias in output variables (Kicklighter et al., 1994; Wollenweber, 1995; Arain et al., 1999).

Plant physiological processes have been scaled-up from cells to the entire canopy to assess carbon exchanges between the canopy and the atmosphere (Farquhar et al., 1980; De Pury and Farquhar, 1997). Several stand-level process-based models have been built and simulate canopy photosynthesis, soil heterotrophic and autotrophic respiration, energy budget and water balance (Running and Gower, 1991; Rasse et al., 2001; Kramer et al., 2002; Dufrêne et al., 2005). These models have also been evaluated through comparison with eddy flux measurements (Law et al., 2000; Baldocchi and Wilson, 2001; Clark et al., 2001; Kramer et al., 2002; Rasse et al., 2001; Arain et al., 2002; Churkina et al., 2003; Ogée et al., 2003; Davi et al., 2005). Regional and global models often estimate the carbon balance using the same algorithms (Sellers et al., 1997) but with a broader resolution, typically at least 50 km \times 50 km, in order to be coupled with a global circulation model (GCM). To date, however, model parameterisation is based on studies performed at the stand level or using remotely sensed data, and is homogeneously applied at broader scales using spatial aggregation of the input parameters. In this article, the term "spatial aggregation" is used when the arithmetic mean of a parameter is used instead of its explicit distribution for a specific area. The error due to the spatial aggregation of input parameters is rarely quantified using both ground data measurements and process-based models. In this context, analysis of carbon and water balances of ecosystems at landscape and regional scales is extremely important, since simulations made at these scales can provide a theoretical framework useful for evaluating the aggregation effect on global models simulations.

In this paper, a process-based model (CASTANEA; Dufrêne et al., 2005) was used to evaluate the effect of aggregating spatial parameters on modelling carbon and water fluxes in temperate deciduous forests. Each submodel of this model was accurately evaluated in a beech ecosystem by comparison to eddy flux measurements, to individual fluxes (soil, wood respiration and branch photosynthesis) and to tree growth data (Davi, 2004; Davi et al., 2005). The fact that this model was validated at the stand level for most of the elementary processes, improves the model's reliability, validity and applicability.

To begin, a sensitivity analysis was carried out to get the response of gross primary production (GPP), ecosystem respiration (R_{eco}) and transpiration (TR) to six ecosystem "parameters", aboveground wood biomass (*B*), available soil water storage or soil water reserve available for the tree (S_{WR}), canopy clumping factor (C_F), leaf area index (*L*), leaf mass per area of sunlit leaves (M_{sun}) and leaf nitrogen content (*N*). Based



Fig. 1. Presentation of the three case studies.

on the sensitivity analysis, the ecosystem parameters among the six defined above were determined, for which the simulated carbon and water fluxes exhibited a non-linear response.

Next, the error caused by aggregating the parameters was quantified in three beech forests at three different scales (subplot, stand and landscape, see Fig. 1). For each of them, the spatial variability of the six ecosystem parameters described above and the budburst date (only in one case study) were quantified using ground measurements. The subplot scale (0.8 ha), was covered by a highly heterogeneous natural (i.e., not managed) stand (named La Tillaie hereafter) located in the Fontainebleau forest (south-east of Paris). The standlevel study was based on a sample of nine plots representative of the Hesse forest (60 ha-north-east of France). Carbon dioxide, water vapour, and energy exchange were measured using the eddy covariance technique (Granier et al., 2000a). At the landscape level, the spatial variability was estimated using a sample of nine beech stands (average area of 8.7 ha) in the southern Fontainebleau forest. Comparisons with tree growth measurements were previously carried out (Barbaroux, 2002; Davi, 2004; Le Maire et al., 2005). Carbon and water fluxes were simulated using CASTANEA both on each individual plot and on a "virtual" plot where averaged input parameters were applied. The effect of spatial aggregation of parameters was tested by comparing simulations using averaged parameters to averaged values of the simulations using plot specific parameters.

2. Materials and methods

2.1. Sensitivity analysis of key model parameters

2.1.1. Model description

CASTANEA is a multi-layer process-based model that is used to predict the carbon, water and energy balance in temperate forests (Dufrêne et al., 2005). The main output variables are: (i) state variables (leaf

area index evolution, biomass of above- and belowground tree compartments, soil carbon and water content) and (ii) flux density variables (canopy assimilation, maintenance and growth respiration, organ growth, soil heterotrophic respiration, transpiration, and evapotranspiration). A canopy is assumed to be homogeneous horizontally, and vertically subdivided into a variable number of layers (i.e., multilayer canopy model), each of them enclosing the same amount of leaf area (0.1 m² m⁻²). No variability is assumed between trees and one "averaged" tree is considered to be representative of a given area. Three different radiative balances are performed, in the PAR [400-700 nm] in the NIR [700-2500 nm], and in the thermal infrared. Canopy clumping is taken into account in the model of radiative transfer by using a clumping factor $(C_{\rm F})$. This factor reduces the leaf area used by the SAIL sub-model (Verhoef, 1984, 1985) to compute radiation interception for each leaf layer. Gross canopy photosynthesis is calculated every half hour following Farquhar et al. (1980) coupled with a stomata conductance model according to Ball et al. (1987). The nitrogen effect of leaves on photosynthesis is taken into account assuming a linear relationship between the maximal carboxylation rate (V_{cmax}) , and the leaf nitrogen content per unit area $N_{\rm a}$, and a fixed ratio between $V_{\rm cmax}$ and the potential rate of electron flow (V_{imax}) . The leaf nitrogen concentration (per mass) N (g(N) g(DM)⁻¹) is assumed to be constant inside the canopy. The leaf nitrogen per unit leaf area $Na(g(N)m_{leaf}^{-2})$ is then calculated for each layer from the leaf mass per area (M_L) profile, which decreases exponentially within the canopy $(M_{sun}$ is the leaf mass per area of sunlit leaves and k_{LMA} the exponential coefficient):

$$M_{\rm L} = M_{\rm sun} \exp(-k_{\rm LMA} L) \tag{1}$$

$$N_{\rm a} = M_{\rm L} N \tag{2}$$

Photosynthesis is computed for developed leaf area by square meter of soil, that is to say the leaf area index (L),

while PAR interception is computed using the effective leaf area ($C_{\rm F} \times L$). Maintenance respiration depends on biomass (B), temperature and nitrogen content of various organs (Ryan, 1991); whereas growth respiration depends on fixed construction costs which in turn depend on organ type (Dufrêne et al., 2005). Heterotrophic respiration $(R_{\rm h})$ is derived from a soil organic carbon sub-model (based on the Century model from Parton et al., 1987). Heterotrophic respiration mainly depends on temperature and soil water content. Spatial variability of soil water content depends also of litter fall, which depends on leaf area index and branch and coarse root mortality (Epron et al., 2001). The big-leaf Penman-Monteith equation (Monteith, 1965) is applied to calculate both transpiration (TR) and evaporation. The soil water balance model is a bucket-type model with three layers. During a water stress period, the slope of the relationship, proposed by Ball et al. (1987) between leaf assimilation and stomatal conductance is assumed to decrease (Sala and Tenhunen, 1996). In CASTANEA, this slope is linearly linked with the relative extractable water (REW) when it falls below a threshold of 0.4 (Granier et al., 1999, 2000b). A complete description of the model and its parameterisation for a beech stand is given in Dufrêne et al. (2005). The modelling of each individual processes were evaluated for the Hesse flux site (Davi et al., 2005) by comparison with local (respiration chambers and branch bags) and flux (eddy covariance techniques) measurements. The main species-specific input parameters are given in Table 1 for beech.

2.1.2. Model simulations

The response of carbon and water flux to six key input parameters that characterise the spatial variability of forest ecosystems were first assessed through sensitivity analysis. Seventeen key input parameters (which include the two initialized state variables) have

Table 1

Main input parameters of CASTANEA for Fagus sylvatic	a]	L
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been previously obtained trough an uncertainty analysis (Dufrêne et al., 2005). Among these 17 parameters, 6 spatially variable structural and biochemical parameters were retained for the sensitivity analysis: stand biomass (B), soil water reserve (S_{WR}) , clumping factor (C_F) , leaf area index (L), leaf mass per area of sunlit leaves (M_{sun}) and nitrogen content per mass unit (N). For each of the six parameters, five values were used in the range of values commonly observed in beech ecosystems, for the sensitivity analysis (Table 2). All combinations between the key input parameters were tested. Simulations were performed using 6 years of meteorological data in Fontainebleau (1994-1999) including various meteorological conditions. The mean response of four variables (GPP, Reco, NEP and TR) to these input parameters over the 6 years was analysed. For each output variable, the average response curve to each input parameter is shown (Figs. 2-4). For one value of a given parameter the other five parameters can have all the possible values (i.e., 5^5 values for a given output variable). Mean and standard deviations were then calculated. In total, $6 \times 5^6 \cong 100,000$ simulations were performed with the CASTANEA model.

2.2. Effect of spatial variability of measured biophysical parameters: three case studies

2.2.1. Characteristics of sites

2.2.1.1. Fontainebleau forest and La Tillaie plot. -Fontainebleau forest (17,000 ha) is located south east of Paris, France (48°25'N, 02°40'E, elevation 120 m). The dominant forest species are oak (*Quercus petraea* (Matus) Liebl., *Quercus robur* (Matus) Liebl.), beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.). The climate is temperate with a mean annual temperature of 10.6 °C and a mean annual rainfall of 750 mm. This forest is managed by the French National Forest Office

	Value	Unit	References
	Varue	om	References
Slope of the dependency between V_{cmax}^{a} and leaf nitrogen density	20	$\mu mol(CO_2) g(N)^{-1} s^{-1}$	Liozon et al. (2000)
Ratio between V_{cmax} and V_{jmax}^{b}	2.1	Dimensionless	Liozon et al. (2000)
Quantum yield	0.292	mol electrons (mol quanta) $^{-1}$	Ehleringer and Björkman (1977)
Curvature of the quantum response of the electron transport rate	0.7	Dimensionless	Fixed
Slope of the ball relationship	11.8	Dimensionless	Medlyn et al. (2001)
Temperature effect for respiration (Q_{10})	1.84	Dimensionless	Damesin et al. (2002)
Nitrogen dependency for all organs	5.5e-4	$mol(CO_2) g(N)^{-1} h^{-1}$	Ryan (1991)

^a Maximum carboxylation rate.

^b Potential rate of electron flow.

Table 2 Range of input parameter values used for the sensitivity analysis

Parameter	Symbol	Unit	Minimum value	Maximum value
Nitrogen content of leaves per mass unit	Ν	% g(N) g(DM) ⁻¹	1.5	3
Leaf mass per area of sunlit leaves	$M_{\rm sun}$	$g(DM) m^{-2}$	80	120
Leaf area index	L	$m^2 m^{-2}$	1	8
Clumping factor	$C_{\rm F}$	Dimensionless	0.45	1
Soil water reserve	S _{WR}	mm	80	250
Biomass of aerial wood	В	$kg(C) m^{-2}$	1	15

(ONF), old growth plot excepted. The soil is mainly sandy.

Spatial heterogeneity in a natural, old, 36 ha portion of the Fontainebleau forest (La Tillaie 48°43'N, 2°68'E, elevation 120 m) was investigated. This forest area has been protected for royal hunting since the 17th century and has not been subjected to forestry practices since that time. The canopy structure showed a very high heterogeneity, horizontal and vertical, due to numerous canopy gaps caused by wind throw (Pontailler et al., 1997). As a result, the canopy structure and light environment were much more variable here than in a managed stand. In this old forest mainly dominated by beech, an area of 80 m \times 100 m (0.8 ha) was delimited. This selected area was characterised by a gradient in the canopy openness, from a clearing in the west to a dense pole stand in the east. The area was staked out every 10 m (99 stakes) allowing the delimitation of 80 squares of 100 m². The average density was 659 stems ha^{-1} . The soil types were luvisol and podzosol (Pontailler, 1979) with calcareous substratum at about a 1-m depth and humus types ranging from mull to moder.

Nine beeches were also sampled in the southern part of this forest. These stands represent a gradient from young to mature forests (i.e., from 30 to 135 years old). Stem densities range from 639 to 5053 stems ha^{-1} and stand areas from 5.6 to 14.7 ha. The soil type is mainly gray Luvisol with a large range of humus type from acid mull to moder. The nine stands sampled are representative of the ecosystem variability of beech stands in the southern forest in terms of canopy characteristics, age and fertility. However, the stands underrepresent the variability of forest on the whole 17,000 ha. For example, the stands dominated by seed bearers were not represented in this sample. For that reason, this sample was considered to only be representative of 500-1000 ha of forest landscape. For more details see Le Dantec et al. (2000).

2.2.1.2. Hesse forest. Hesse forest (60 ha, four stands) is located in eastern France ($48^{\circ}40'$ N, $7^{\circ}05'$ E, elevation 300 m). It is mainly composed of beech with a very

sparse understorey. The plot where the flux tower was installed covers 0.63 ha of a young beech forest (33 years old in the year 2000) with a density of 3482 trees ha⁻¹ and a dominant height close to 15 m. The soil type was intermediate between luvisol and stagnic luvisol, with a hydromorphic layer and clay content ranging from 25 to 40%. The annual precipitation was 820 mm and the average temperature 9.2 °C. For more details, see Granier et al. (2000a). Since 1997, CO₂ flux has been measured at 18 m (i.e., 3 m above the canopy) on a meteorological tower using the eddy covariance method (Leuning and Moncrieff, 1990).

A grid with a resolution of 50 m and covering 60 ha was installed around the Hesse site (CARBOEUROPE site). One hundred and eighty two plots were then defined. Soil type and leaf area index were estimated on the 182 plots (Bouriaud et al., 2003). In addition to the CARBOEUROPE site, eight plots were sub-sampled (average area of 835 m^2) inside the three surrounding forest units, which include the footprint of the eddy covariance measurements (Bouriaud, 2003; Bouriaud et al., 2003). The plots were selected in order to reflect the highest variability in terms of leaf area index (L) and soil type (Bouriaud et al., 2003). The L variability among plots was caused by a recent forest thinning on five out the nine studied plots. Beech represented more than 75% of the total basal area. The other tree species were hornbeam (Carpinus betulus Liebl.), sessile oak (Q. petraea, Matt. Lieb.) and silver birch (Betula pendula Liebl). Eight plots were 30-40 years old, and one plot was 50 years old.

2.2.2. In situ measurements of main canopy characteristics

2.2.2.1. First case study at the subplot scale: "La Tillaie". The leaf area index (L) and the clumping factor (C_F) were estimated above the 99 stakes (every 10 m) by using hemispheric photographs. The photographs were taken at 1.5 m above the ground using a digital camera (CoolPix 950, Nikon Corporation, Tokyo, Japan) equipped with a fisheye lens. The images were recorded in FINE mode (slightly compressed in



Fig. 2. Sensitivity analysis of annual gross primary production (GPP), net ecosystem production (NEP), ecosystem respiration split into the autotrophic respiration (solid line) and the heterotrophic respiration (dashed line) and transpiration (TR) to: (a) leaf area index (L) and (b) clumping factor (C_F). Carbon fluxes are expressed in g(C) m⁻² year⁻¹ and water fluxes in mm year⁻¹. Vertical bars are the standard deviation of the ensemble of simulations.



Fig. 3. Sensitivity analysis of gross primary production (GPP), net ecosystem production (NEP), ecosystem respiration split into the autotrophic respiration (solid line) and the heterotrophic respiration (dashed line) and Transpiration (TR) to: (a) leaf mass per area of sunlit leaves (M_{sun} in g(DM) m⁻²) and (b) leaf nitrogen content per biomass unit (N in %). Carbon fluxes are expressed in g(C) m⁻² year⁻¹ and water fluxes in mm year⁻¹. Vertical bars are the standard deviation of the ensemble of simulations.



Fig. 4. Sensitivity analysis of gross primary production (GPP), net ecosystem production (NEP), ecosystem respiration split into the autotrophic respiration (solid line) and the heterotrophic respiration (dashed line) and Transpiration (TR) to: (a) stand aerial biomass (*B* in kg (C) m⁻²) and (b) soil water reserve (S_{WR} in mm). Carbon fluxes are expressed in g(C) m⁻² year⁻¹ and water fluxes in mm year⁻¹. Vertical bars are the standard deviation of the ensemble of simulations.

JPEG, no effect was observed) with a 1600×1200 pixel resolution. Measurements were made on cloudy days to prevent multiple scattering effects caused by direct radiation. Using Adobe PhotoshopTM, a threshold process was applied to several areas of each photograph using the threshold intensity for RGB images. The best calibration data determined for the Nikon Coolpix 950 was used to divide the photograph into sectors of 10° of azimuth angle (ω_i) and 5° of the zenith angle (θ_i). The gap fraction (P) was estimated using Gap Light Analyser Software (Frazer et al., 2000). Then L and $C_{\rm F}$ were calculated following methods in van Gardingen et al. (1999). For the L calculation, the first 45° of the zenith angles were used. Based on van Gardingen et al. (1999) an "equivalent" leaf area index $(L_{\ln av})$, assuming no clumping in the azimuth (Eq. (3)) and a "true" leaf area index (L) taking into account this clumping (Eq. (4)), were calculated. The ratio between the two estimates (Eq. (5)) provided the clumping factor $(C_{\rm F})$. $C_{\rm F}$ was low when the canopy was clumped. To prevent a logarithm of zero, a minimum gap fraction of one pixel was assumed.

$$L_{\ln av} = -\frac{2\sum_{i=1,9}\ln P(\theta)\cos(\theta_i)\sin(\theta_i)}{1-\cos(\pi/4)}$$
(3)

$$L = -\frac{2\sum_{i=1,9}\sum_{j=1,36}\ln P(\theta_i,\omega_j)\cos(\theta_i,\omega_j)\sin(\theta_{i,j},\omega_j)}{1-\cos(\pi/4)}$$

$$C_{\rm F} = \frac{L_{\ln av}}{L} \tag{5}$$

L and $C_{\rm F}$ were then estimated over the 80 squares by interpolation using the weighted inverse distance centred on each stake with a 10 m radius. Average L and $C_{\rm F}$ were then determined over the 80 squares.

Diameter at breast height, tree height and geographic position were measured for the 527 trees in the study area. From these measurements, aboveground wood biomass was estimated using allometric relationships (Bouchon, 1982; Barbaroux et al., 2003). Tree age was also assessed from allometric relationships between tree height and tree age (Davi, 2004). Living biomass that drives simulated respiration was quantified by using a relationship between tree age and the proportion of living biomass (Barbaroux, 2002; also see Section 2.1.1).

One hundred and sixty two samples, each with 10 leaves, were obtained from 27 trees at various heights (by shooting twigs with a rifle), in order to estimate leaf mass per area and nitrogen (N) content per mass unit. The leaf area was measured using a leaf area meter

(Delta-T Area meter, Delta-T Devices, Cambridge, UK). The leaves were dried (60 °C), ground into powders and weighed to obtain dry leaf mass. Next an elementary analyser (Thermo-Quest NCS 2500, France) was used to obtain nitrogen and carbon content according to Dhum's method. A linear relationship was found between N and L of the square where the leaves were sampled:

$$N = 0.20L + 2(n = 27)$$

This relationship was then used to estimate the nitrogen content of leaves in each of the 80 squares. A measured average value of 98 g(DM) m⁻² ($\sigma^2 = 12$ g(DM) m⁻²) was used (Davi, 2004), because no significant spatial variation of M_{sun} was found.

Soil types were surveyed for the entire reserve of "La Tillaie" (Bouchon et al., 1973; scale: 1/1000). The volumetric soil water content at the wilting point (θ_{wilt}), at field capacity (θ_{fc}), and soil depth (H_{soil}), were measured on this site for the two main soil types: podzosol and grey Luvisol (Pontailler, 1979). θ_{fc} was determined in situ in March (during the leafless period) at the end of a rainy winter (March) but following 2 weeks without rain. Soil samples were obtained using 250 cm³ steel cylinders and they were dried at 105 °C until a constant weight, so soil moisture per unit volume and weight, and soil bulk density could be determined. Soil moisture at wilting point was determined following equilibrium in a pressure membrane extractor at 15 bar (Soil Moisture, Santa Barbara, CA, USA). The abovementioned bulk density values were used to calculate moisture values per unit volume. Both determinations were performed along vertical profiles, at 10-cm intervals, with three replicates per layer. The available water storage, called soil water reserve (S_{WR}) hereafter, was then estimated from these measurements as follows:

$$S_{\rm WR} = H_{\rm soil}(\theta_{\rm fc} - \theta_{\rm wilt})$$

2.2.2.2. Second case study at the stand level: the Hesse forest (CARBOEUROPE site). On the nine selected plots, L was measured using litter collection and two optical methods: hemispherical photographs and a Plant Canopy Analyser (PCA LAI-2000, Li-Cor, Nebraska, USA). Leaf litter was collected in 0.5 m² square-shaped traps on three pick-up days, respectively days of year 291, 304 and 325 (see Bouriaud et al., 2003 for details). PCA measurements were performed using two inter-calibrated sensors in the middle of June, when maximum leaf expansion was achieved and at sunset or sunrise to avoid direct sunlight. L was calculated using

C2000 software (Li-Cor, Nebraska, USA) and the three upper rings to provide a better agreement with litter collection (Fassnacht et al., 1997; Dufrêne and Bréda, 1995; Planchais and Pontailler, 1999). The hemispherical photographs were taken and analysed for each of the nine plots using the protocol described in the first case study. The *L* estimates using litter collection were then used for the simulations. In this case study, the estimations of *L* by litter collections permitted the evaluation of the two indirect methods (*PCA* and hemispherical photographs). The results were discussed in Bouriaud (2003) and Davi (2004).

Diameter at breast height was measured on all trees inside the plots. Tree volume and biomass were then estimated from tree diameter using allometric relationships that were established on the same site (Le Goff and Ottorini, 2001).

Using the methodology described in the first case study, the leaf mass per area and the foliar nitrogen content per mass unit were estimated using samples of 10 sunlit leaves per tree for six trees in each of the nine plots.

A pedological study was carried out on the same site (Quentin et al., 2001). Several drilled pits enabled the determination of the chemical and physical properties of the soil. The different soil types were determined and a classification of the nine plots according to their soil type was established (Bouriaud et al., 2003). From these measurements, the soil water reserve was determined in each plot following the method described in the first case study. Finally, the date of budburst was determined for each of the nine plots in the year 2000.

2.2.2.3. Third case study at landscape level: the southern part of Fontainebleau Forest. L was estimated using ground measurements performed in 1996. The measurements were made using PCA (LAI-2000) between June and mid-July, and the L estimation was performed using the three upper rings. For each stand and according to its size, 40-150 LAI-2000 measurements were taken at intervals ranging from 5 to 10 m and on several transects. See Le Dantec et al. (2000) for a precise description of those measurements. The spatial variability of the clumping factor was not assessed in this last case study and an average measured value of 0.79 was used (data not shown).

During the winter of 1995–1996, the distribution of the stem diameters was measured in every stand. Tree volume in each diameter class was assessed by allometry according to Bouchon (1982) and converted into biomass using wood density measurements (Barbaroux et al., 2003). The aboveground wood biomass was then calculated from the diameter distribution and the tree biomass in each diameter class. For further details see Barbaroux (2002).

The biochemical and biophysical characteristics of leaves were determined in July 1996, using samples of 10 sunlit leaves and 10 shaded leaves on five trees per stand. Nitrogen content and leaf mass per area were then determined using the method described in the first case study (see above).

A soil database was built by the French National Forest Office in 1995. It relies on about 8600 drilled pits evenly distributed within the Fontainebleau forest (one every 2 ha). The samples were obtained using a 2-m manual drill. Attributes given to each point included soil and humus type, and the underlying parent material and its depth, and for each horizon the type, depth, texture, proportion of coarse elements, effervescence and pH. The nomenclature of soil and humus types was based on Duchaufour (1982). The texture was determined by hand. From soil depth and texture, the soil water reserve (S_{WR}) was estimated according to Saxton et al. (1986). Then S_{WR} was spatially estimated for the Fontainebleau forest using the inverse distance weighted interpolation method for two adjacent points. The average values of $S_{\rm WR}$ in the nine studied plots were estimated from the $S_{\rm WR}$ map covering the entire forest. A description of this methodology is given in Le Maire et al. (2005).

In the three case studies, the carbon input and the soil texture was used to estimate the initial soil carbon content, by assuming a steady-state hypothesis. Under this hypothesis, for each soil carbon pool, the same annual amount of carbon enters and leaves the pool.

2.2.3. Plan of simulations

The variability of the key input parameters measured in situ in the three case studies enables: (i) the estimation of the variability of four output variables: gross primary production (GPP), ecosystem respiration (R_{eco}) , carbon net ecosystem production (NEP) and tree transpiration (TR), and (ii) the determination of the main input parameters, which explained the water and carbon fluxes variability. For each site, simulations were performed for two contrasted years with regard to rainfall during the leafy period: 1996 was a dry year (from early May to the end of September, 200 mm of rain fell in Fontainebleau, and 264 mm fell in Hesse) with a pronounced soil water shortage, while 2000 was wetter year (440 mm of rain fell in Fontainebleau and 514 mm in Hesse), even though the soil water stress sill occurred in the year 2000 (but to a lesser degree).

(i) For the three sites, CASTANEA was used to estimate carbon and water flux in each plot, with k

variable input parameters named X (Table 5). Eighty sets of simulations were performed for la Tillaie (n = 80; k = 5), whereas nine sets of simulations were performed for Hesse (n = 9; k = 8) and for Fontainebleau (n = 9; k = 5). Then, for each case study, using these n simulations, the average and standard deviation of each of the four output variables (Y) were calculated. The standard deviation, named σ_{base} hereafter, was used as an estimate of the spatial variability of a given output variable:

$$\sigma_{\text{base}} = \frac{1}{n-1} \sqrt{\sum_{i=1,n} \left(Y(\text{all } X)_i - \overline{Y(\text{all } X)} \right)^2}$$

(ii) For each study case, the average values of *k* key input parameters were fixed, while the *k*th remained free (named hereafter X_j). A new standard deviation of each output variable was calculated ($\sigma_{\text{par } X}$).

$$\sigma_{\text{par}X} = \frac{1}{n-1} \sqrt{\sum_{i=1,n} \left(Y(\text{only}X_j)_i - \overline{Y(\text{only}X_j)} \right)^2}$$

The comparison of the different standard deviations, calculated when only one parameter was variable, indicated which parameter contributed the most to the variability of the output variables considered. Results were represented with piled histograms (Fig. 6). σ_{base} was also compared with σ_{sum} as follows:

$$\sigma_{\rm sum} = \sqrt{\left(\sum_{X=1,k} \left(\sigma_{\rm parX}\right)^2\right)}$$

The difference between σ_{sum} and σ_{base} was used to evaluate the compensatory effects between parameters. If the sum of the standard deviations, obtained when one input parameter is variable (σ_{sum}), is superior to the standard deviation obtained when all parameters are variable (σ_{base}), we can assume that some compensations between parameters occurred.

2.3. Comparison of model outputs using spatially variable and aggregated parameters

For each case study, a final simulation was performed with the average values of the input parameters. The comparison of the outputs variables, which were simulated when all parameters varied spatially, to this last simulation, allowed quantification of the effect of the aggregation of input parameters. In addition, the simulated daily NEP and the relative extractable water (REW) for Hesse the year 2000, were also compared to the NEP measurements performed by the eddy covariance technique (Granier et al., 2000a) and to the REW, that was measured weekly with a neutron probe (Granier et al., 2000b). These last simulations permitted the evaluation of the model and the analysis of the effect of the spatial parameters aggregation on a daily basis.

3. Results and discussion

3.1. Sensitivity analysis of key model parameters

The gross primary production (GPP) and the transpiration (TR) increase with leaf area index (L), with saturation for the high L values (Fig. 2a). Ecosystem respiration (R_{eco}) increases almost linearly with L (mainly due to a linear increase of heterotrophic respiration), and consequently, the NEP (i.e., difference between GPP and R_{eco}) increases until L reaches a value of 5 and then shows a plateau above 5. GPP, R_{eco} and NEP, all decrease slightly when the canopy clumping $(C_{\rm F})$ increases, but this effect is small in comparison to the other effects (Fig. 2b). When the canopy clumping increases (i.e., $C_{\rm F}$ decreases), there is more light available to the lower parts of the canopy, which improves the light use efficiency at the canopy scale. For that reason, for the same L, low $C_{\rm F}$ values contribute to higher GPP. This result agrees with the study by Law et al. (2001), in which the simulated GPP was stimulated when the clumping was taken into account in their model. The raise of the leaf mass per area of sunlit leaves (M_{sun}) or of the leaf nitrogen content (N), leads to a positive linear effect on the four fluxes (i.e. GPP, R_{eco} , NEP and TR, Fig. 3a and b). These two parameters have a similar effect on GPP, an effect which nevertheless remains smaller than the effect of L (Figs. 2a and 3a and b). In theory, a strong increase of $M_{\rm sun}$ and N should lead to a plateau in GPP by saturation as the increase of photosynthetic capacities cannot be infinite. In CASTANEA however, the sensitivity of GPP to M_{sun} and N is linear, which can indeed be true for the range of observed values. Finally, the increase of the above ground biomass (B) has no effect on GPP but a strong positive non-linear effect on autotrophic respiration (R_a) . The non-linearity is due to a non-linear relationship between aboveground biomass and the proportion of living cells in the wood (Barbaroux, 2002). Because few data exist concerning the evolution of this proportion with age (Ceschia et al., 2002), the response of R_a to above ground biomass remains uncertain. Nevertheless, we know qualitatively that the autotrophic respiration increases more slightly than the aboveground biomass (Ryan and Waring, 1992),

which causes a saturation plateau for large values of aboveground biomass. NEP shows a non-linear decrease with *B* (Fig. 4a). The increase of soil water reserve (S_{WR}) leads to an increase in GPP, NEP, TR and to a lesser extent of R_{eco} (Fig. 4b). To conclude, three main causes of non-linearity were highlighted by the sensitivity analysis: high values of *L* for GPP, high and low values of *B* for R_{eco} and to a lesser extent, the high values of S_{WR} for GPP.

3.2. Effect of spatial variability of measured biophysical parameters: 3 case studies

3.2.1. First case study: La Tillaie

The *L* showed a strong variability between a clearing in the southwest of the area where *L* ranges from 0.75 to 2.5 and a dense canopy at the north and east where *L* reached values higher than 8 (Fig. 5). The average value of *L* on the surface of 0.8 ha was 5.79 ($\sigma^2 = 1.21$). Clumping was



Fig. 5. Spatial distribution over the 80 squares of 100 m² in the Tillaie of the measured "true" leaf area index (*L*), clumping factor (*C*_F), aboveground biomass (*B* in kg(C) m⁻²) and soil water reserve (*S*_{WR} in mm) and the simulated net ecosystem production (NEP in g(C) m⁻² year⁻¹) and transpiration (in mm year⁻¹) using meteorological data from 2000.

Table 3 Main stand specific input parameters in nine beech plots in Hesse forest

N ^a (%)	M_{sun}^{b} (g(DM) m ⁻²)	$\frac{L^{c}}{(m^2 m^{-2})}$	Clumping (C _F)	S _{WR} ^d (mm)	$B^{\rm e}$ (g(C) m ⁻²)	Budburst date	Age	Plot area (m ²)
2.25	91	7.89	0.74	130	6192	120	30	0.07
2.62	74	6.73	0.80	130	6765	120	30	0.08
2.38	88	7.52	0.66	130	5311	117	30	0.09
2.32	91	4.72	0.53	105	5079	114	30	0.07
2.53	76	4.67	0.55	86	5787	114	30	0.09
2.62	85	4.70	0.55	149	4857	114	30	0.08
2.56	81	5.89	0.61	140	4741	115	30	0.06
2.38	83	6.91	0.55	140	7714	116	50	0.14
2.38	83	7.30	0.66	140	5135	114	30	0.12

^a Nitrogen content.

^b Leaf mass per area of sunlit leaves.

^c Leaf srea index.

^d Soil water reserve.

^e Stand aerial wood biomass.

generally larger when *L* was lower (Fig. 5). The spatial distribution of the canopy clumping presented a west to east gradient. The average clumping factor (C_F) was 0.62 with values ranging from 0.38 to 0.81 ($\sigma^2 = 0.10$). Biomass reached a high average value of 14,900 g(C) m⁻² and showed strong spatial variations (coefficient of variation of 108%), mainly due to the variations of stem density and tree age (data not shown). Soil water reserve (S_{WR}) showed little variation from 120 to 140 mm, with smaller values in the northern part of the stand.

3.2.2. Second case study: Hesse

The leaf nitrogen content per mass unit (*N*) ranged from 2.25% to 2.62% (Table 3), but its variability was negatively correlated to the leaf mass per area (M_{sun}) of sunlit leaves (R = -0.76). Consequently, the leaf nitrogen content per surface unit ($N_a = M_{sun} \times N$), which controls

Main stand specific input parameters in nine beech stands in Fontainebleau forest

photosynthesis, was less variable. L ranged from 4.67 to
7.89; this variability was partly explained by a thinning,
which occurred in January 1999, in five plots. This thin-
ning increased the heterogeneity of the canopy structure
and explained the clumping variability. Clumping factor
$(C_{\rm F})$ ranged from 0.55 to 0.80 in the nine plots (Table 3).
Its average value was 0.60 in the thinning area and 0.70
outside. S _{WR} exhibited stronger variations in Hesse than
in La Tillaie, and ranged from 86 to 149 mm, with an
average value of 130 mm. Small S_{WR} values could also
contribute to explaining the lower L values in plots 73 and
75. Both the age of trees and the thinning were responsible
for the spatial variability of aboveground biomass, which
varied from 4741 to 7714 g(C) m^{-2} (Table 2). The plot
where trees were 20 years old of greater than in the other
plots, had a stronger aboveground biomass (+30%) and
thinned plots had a lower biomass (-19%) .

N ^a (%)	$M_{\rm sun}^{\rm b}$ (g(DM) m ⁻²)	$L^{\rm c} ({\rm m}^2{\rm m}^{-2})$	$S_{\rm WR}^{\rm d}$ (mm)	$B^{\rm e}$ (g(C) m ⁻²)	Age	Stand area (ha)
2.39	109	4.69	99	5021	46	6.6
2.33	115	4.94	112	6514	48	6.0
2.74	102	6.49	115	4194	44	8.2
2.29	97	4.95	126	11876	79	8.6
2.40	96	6.10	136	5570	80	10.4
2.19	113	6.60	101	4423	28	5.6
2.26	90	3.80	101	13628	131	11.8
2.50	104	7.83	106	2912	33	6.7
2.80	106	7.61	133	3494	29	14.7

^a Nitrogen content.

Table 4

^b Leaf mass per area of sunlit leaves.

^c Leaf area index.

^d Soil water reserve.

^e Stand aerial wood biomass.

3.2.3. Third case study: Fontainebleau

N ranged from 2.19% to 2.80% (Table 4). This variability was stronger in Fontainebleau than in Hesse forest. M_{sun} ranged from 96 to 115 g(DM) m⁻² and the average value of 103 g(DM) m⁻² was close to the value found in La Tillaie (98 g(DM) m⁻²) but stronger than in Hesse (83 g(DM) m⁻²). *L* ranged from 3.80 to 7.83 and S_{WR} from 99 to 136 mm. The aboveground biomass showed a large variability ranging from 2912 to 13,628 g(C) m⁻².

The variability of the different parameters, measured in the three case studies, was estimated using the coefficient of variation. By comparing the three cases, the variability of the aboveground biomass was higher in La Tillaie, while the soil extractable water showed a greater variability in Hesse and in Fontainebleau. Finally N and M_{sun} showed few spatial variations comparatively to the other parameters (Table 5).

3.2.4. Effect of the measured variability on the simulated outputs

In La Tillaie, the spatial variability of simulated NEP mainly correlated the aboveground biomass, while *L* and S_{WR} seemed to control the spatial variability of TR (Fig. 5). *L* variability also explained 82% of the hetero-

Table 5

Coefficient of variation (CV in %) of the different input parameters in the three case studies

Parameters	Symbol	Tillaie	Hesse	Fontainebleau
Leaf area index	L	14	21	23
Clumping factor	C_{F}	12	15	_
Leaf mass per area of sunlit leaves	M _{sun}	-	7	8
Foliar nitrogen concentration	Ν	6	6	9
Aerial wood biomass	В	108	17	59
Soil water reserve	$S_{\rm WR}$	5	16	12
Budburst date	Bud	-	2	-

trophic respiration variability (data not shown). However, the strong variation of the aboveground biomass implied high local variations of the R_a that masked the effects of the other parameters acting on photosynthesis (N, L and C_F) or on heterotrophic respiration (i.e., L). Consequently, the standard deviation of R_{eco} on the 80 plots was mainly due to the autotrophic respiration (Fig. 6a). This conclusion was strengthened by the analysis of causes of spatial variability in which the impact of varying the spatial parameters are tested one by one. The aboveground biomass variability alone explained 62% of the



Fig. 6. Standard deviations of gross primary production (GPP), net ecosystem production (NEP), ecosystem respiration (R_{eco}) and transpiration (TR) simulated when spatial parameters are varying one by one during a wet year (2000). The total variability is thus shared out into the various components: leaf area index (L), clumping factor (C_F), leaf mass per area (M_{sun}), leaf nitrogen content (N), aboveground biomass (B), soil water reserve (S_{WR}) and budburst date (bud).

total variability of the NEP, while *L* and S_{WR} explained 76% of the variability of TR (Fig. 6a). There were compensatory effects between the input parameters for the NEP, as the σ_{sum} (181 g(C) m⁻² year⁻¹) was stronger than the σ_{base} (154 g(C) m⁻² year⁻¹). This effect was caused by a positive correlation between *L* and C_F (*R* = 0.73). As the effect of *L* on NEP was positive, while the effect of C_F was negative, a correlation between the two parameters contributed to a compensatory effect. There was also an antagonistic effect of *L* on NEP through the GPP and through heterotrophic respiration (*R*_h), and since *R*_h was positively correlated to the GPP (*R* = 0.89), this also contributed to the compensatory effect. In 2000, the GPP and the NEP were lower in the Hesse forest than in La Tillaie. In the Hesse forest, L, N, M_{sun} and B played similar roles in explaining the NEP variability, while the clumping factor (C_F) appeared to be slightly more important than the other parameters (Fig. 6b). The fact that L and C_F variability was essentially due to the effect of thinning, revealed the importance of theses spatial variation of forestry practices that generate an NEP spatial variability. Higher L, M_{sun} or N led to increases in both the GPP and the R_{eco} , but because the NEP is the difference between GPP and R_{eco} , the effect of these parameters (L, M_{sun} and N) on NEP was reduced. This is not the case for clumping



Fig. 7. Comparison of gross primary production (GPP), net ecosystem production (NEP), ecosystem respiration (R_{eco}) and transpiration (TR) simulated with average parameters and with the average of *n* simulations. Vertical bars are the standard deviation of the *n* simulations. Comparison is carried out at three spatial scales (0.8, 60 and 1000 ha) and in each case for a dry (1996) and a wet year (2000).

factor, which had no effect on $R_{\rm h}$ and few on $R_{\rm eco}$. This suggests its relative importance in explaining the NEP variability. There were some compensatory effects, as $\sigma_{\rm base}$ (74 g(C) m⁻² year⁻¹) was smaller than $\sigma_{\rm sum}$ (107 g(C) m⁻² year⁻¹). $M_{\rm sun}$ was negatively correlated to the nitrogen content, so the $M_{\rm sun}$ variability partly compensated the effect of nitrogen content on the GPP, which explained the compensatory effect.

In Fontainebleau, the simulated GPP was smaller than in la Tillaie. The above ground biomass varied more in Fontainebleau than in Hesse and consequently tends to explain most of NEP variability (Fig. 6c). As in Hesse, the *L*, *N* and M_{sun} effects on NEP, were reduced by their antagonistic effects on NEP through R_{eco} and GPP. There is less compensation between parameters in the NEP variability; indeed σ_{sum} (155 g(C) m⁻² year⁻¹) was closer to the σ_{base} (140 g(C) m⁻² year⁻¹).

3.2.5. Comparison of model outputs using spatially variable and aggregated parameters

In La Tillaie, NEP was strongly reduced in 1996 compared to 2000 (-20%), because of the water stress effect on GPP (Fig. 7a). For the 2 years, there was very little bias when using the simulations with average parameters in comparison to averaging the 80 outputs (Fig. 7a). In the simulation using the average input parameters in 2000, GPP R_{eco} and NEP were slightly overestimated, respectively only, of 28, 11 and 17 g(C) m⁻² year⁻¹. The aggregation effect induces only a +3% bias on the simulated NEP. By analyzing of the simulations when the parameters varied one to one, it was observed that this bias was mainly due to *L* (data not shown). In Hesse, using average input parameters also induces little effect (Fig. 7b). Indeed, in Hesse, a small positive bias on NEP was observed (+24 g(C) m⁻²



Fig. 8. (a) Daily net ecosystem production (NEP) and (b) daily relative extractable water (REW) measured and simulated in Hesse in 2000. One simulation done with the average input parameters (black line) is compared with the average of nine simulations (grey line) done on nine plots from the 60 ha surrounding the flux measurements. The error bar is the standard deviation of the nine simulations.

 $vear^{-1}$ in 2000 and +34 g(C) m⁻² vear⁻¹ in 1996). At a daily time step, the model correctly reproduces the measured NEP (Fig. 8a). The correlation coefficients between daily simulated and measured NEP were equal in the two case studies, with or without aggregation of the input parameters: $R^2 = 0.88$. Moreover, it was difficult to graphically distinguish the two kinds of simulations (Fig. 8). NEP and REW variability between the nine plots represented by the error bar (1S.D.), was small and cannot explain all of the differences between simulated and measured NEP or REW (Fig. 8). In 2000, the annual NEP simulated in the Carboeuroflux plot was equal to the annual measured NEP (438 g(C) m^{-2} year⁻¹). In Fontainebleau in 2000, no bias was observed when the NEP simulated with the average input parameters was compared with the average of nine of each of the stand simulations (+0.4 g(C) m^{-2} year⁻¹). On the contrary, a negative bias was found in 1996 ($-37 \text{ g}(\text{C}) \text{ m}^{-2} \text{ vear}^{-1}$).

When aggregating spatial input parameters, in the three case studies, few biases were found for NEP, and no bias for TR, neither for a dry year nor for a wet year. A positive bias that was produced was expected, due to saturation occurring. For this case the saturation curve was very progressive, which explains the small amplitude of the bias. The effects of non-linear response of NEP to the parameters would have been greater if there had been a real threshold, above which the variability of a given parameter would have had no effect on the NEP. This was not found in the three case studies, but theoretically, this could be the case for the soil water reserve (S_{WR}) or for L at the regional level (Le Maire, 2005). A negative bias on NEP was also found in Fontainebleau during the dry year. This was mainly due to a negligible bias on GPP and a positive bias on R_{eco} . This result showed that different positive biases on GPP and $R_{\rm eco}$ could either induce a positive or a negative bias on NEP according to the site and the year.

4. Summary and conclusion

Using a process-based model, the effects of spatial variability of the main input parameters driving the carbon and water fluxes were investigated. A sensitivity analysis and three case studies were used to determine: (i) which input parameters explained the majority of the spatial distribution of carbon and water flux and (ii) what were the effects of aggregating spatial parameters on the estimation of these fluxes? It was observed that the aboveground biomass explains a great part of net ecosystem productivity (NEP) variability at the small scale (1 ha), and is co-dominant at larger scales (60–1000 ha). Leaf area index (L), Leaf mass per area of sun

leaves (M_{sun}) and nitrogen content in leaves (N) play similar roles, while soil water reserve (S_{WR}) variability seems to be more important at a larger scale (60– 1000 ha). The clumping factor (C_F) variability also influenced the NEP variability; consequently more efforts are required in order to quantify this parameter. Transpiration (TR) varied less spatially than the NEP and its variations were mainly explained by S_{WR} and L.

The most interesting and unexpected result is that despite the non-linear responses of NEP to *L* and to the wood biomass (*B*), a negligible bias was found when input parameters were aggregated. This result tends to prove that the use of process-based model at larger scales in order to couple them with global circulation models, can be justified. It is now necessary to perform similar studies at regional scales ($50 \text{ km} \times 50 \text{ km}$) using remote sensed data for areas that include several dominant species and cover types.

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