The fundamental role of reserves and hydraulic constraints in predicting LAI and carbon allocation in forests

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ABSTRACT

A model simulating forest carbon and water fluxes was improved to simulate carbon allocation to roots, reserves and aboveground woody biomass and to estimate maximum leaf area index of the current year (LAI_{max}). LAI_{max} was calculated from the carbohydrates reserve, which integrates past ecological conditions. Allocation coefficients to the various compartments were originally fixed constant in the basic version, with no temporal and spatial variation. In the improved version, these coefficients were modified spatially and temporally according to functional rules. Carbon allocation to fine roots was simulated by accounting for hydraulic constraints. An empirical model was developed to simulate allocation to reserves. Allocation to aboveground woody biomass was the residual; remaining carbon after allocation to reserves and fine roots. Then, this residual carbon was partitioned into stem diameter and height growth. The allocation model was tested on 20 stands of oak and beech in the Fontainebleau forest. The model reproduced wood growth and LAI_{max} dynamics between 1994 and 1999. While the basic version of the model overestimated the growth (364 g_C m^{-2} year^{-1} vs. 261 g_C m^{-2} year^{-1}) and did not reproduced the growth variability well between sites ($r = 0.4$), the new version better reproduced the average level of growth (235 g_C m^{-2} year^{-1} vs. 261 g_C m^{-2} year^{-1}) and the variability ($r = 0.64$). That model also reproduced the decline of productivity with age and the processes leading to temporal variability in LAI, such as water stress in the previous year.

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1. Introduction

1.1. Improve allocation modelling to bridge the gap between process-based and empirical models

Some process-based models have coupled water vapour and carbon dioxide exchange between vegetation and the atmosphere that explicitly integrate climate effects (Kramer et al., 2002; Dufrêne et al., 2005; Davi et al., 2006c). On the other hand, wood production has been estimated during the last century using statistical models based on empirical field measurements that account for management and age effect (Schober, 1975; Dhote, 1991). To improve predictions of forest production with global change, it has been necessary to couple mechanistic approaches with empirical forestry knowledge (Mäkelä, 1988; Sievänen and Burk, 1993; Johnsen et al., 2001; Landsberg and Waring, 1997; Valentine et al., 1997; Bartelink, 2000; Mäkelä et al., 2000; Landsberg, 2003).

To couple process-based and empirical models, the allocation of carbon between different compartments inside the tree and between the various individuals must be improved (Litton et al., 2007). The allocation of carbon can be simulated either by focusing on the series of carbon translocation processes or solely on the requirements of the tree. Carbon translocation processes include transformation to saccharose, phloem loading, transport by diffusion and unloading to the sinks of maintenance and growth (Thornley, 1972). At the stand level, models based on the potential sink (requirements of the tree) are easier to use. Allocation coefficients can be kept constant for the various compartments (MacMurtrie and Wolf, 1983) or allowed to vary according to site fertility (MacMurtrie, 1985), tree social status (Mäkelä and Hari, 1986) or stand age (Magnani et al., 2000). To model allocation coefficients, a priority system (Bossel, 1987) can be used where carbon is first allocated to leaves (Weinstein and Yanaï, 1994) to reach a level calculated according to allometric laws (Landsberg, 1986), or according to relations between the leaf/root ratio and the nitrogen or magnesium concentration in the soil (Wikström and Ericsson, 1995). Other nutriment limitations could be important: P was the nutrient limiting net primary production in many ecosystems (Herbert and Fownes, 1995; Gradowski and Thomas, 2006) and consequently can also drive the allocation (Ericsson, 1995). The relationships among the functional compartments of a tree (fine roots, large roots, trunk, branches and leaves) are also highly constrained by the need to maintain a hydraulic continuum from fine roots through to the leaves (Shinozaki et al., 1964; Magnani et al., 2000).

1.2. The different approaches for LAI prediction

Leaves are an important carbon sink and leaf area (LAI) and leaf mass (leaf mass per area) are key ecosystems parameters strongly impacting the Net Ecosystem Exchange. Consequently, LAI and LMA modelling are an important challenge. A method to simulate LMA was already given in Davi et al. (2008). Here, we will focus on LAI.

LAI is an index of canopy structure which controls different processes of a forest ecosystem such as light and rain interception (Gash, 1979), gross productivity (Jarvis and Leverenz, 1983; Linder, 1985; Vose and Allen, 1988; Coyea and Margolis, 1994; Maguire et al., 1998) and transpiration (Granier et al., 2000a). In addition, soil respiration which contributes a significant part of carbon fluxes (Granier et al., 2000b; Janssens et al., 2001) is correlated to litterfall (Davidson et al., 2002).

Some models simulate LAI from the carbon budget of the current year (Garcia et al., 1999; Running and Gower, 1991). LAI thus calculated can be corrected according to nitrogen and water availability (Running and Gower, 1991). Another method consists of optimizing LAI to either maximize carbon uptake or limit the effect of drought (Woodward, 1987; Kergoat, 1995).

In this paper, the stand-level model CASTANEA (Dufrêne et al., 2005) was modified to (1) simulate the stand LAI from reserves level and (2) to improve the carbon allocation model by including reserves and hydraulic constraints. The new model is then tested using aboveground biomass and LAI from 20 stands dominated by two different deciduous species in the Fontainebleau forest near Paris.

2. Materials and methods

2.1. The model

2.1.1. General characteristics of the CASTANEA model
CASTANEA is a multi-layer model based on physiological and physical processes simulating carbon, water and energy balances in forest stands. Tree structure was a combination of four functional compartments: leaves, aboveground woody biomass, coarse and fine roots. A reserve compartment is also represented but does not have a physical location.

The canopy was horizontally homogeneous and vertically subdivided into layers. Three radiation balances were calculated: PAR [400-700 nm], total radiation [400-2500 nm], and thermal infrared. Incident light was divided into direct and diffuse radiation using equations given by Spitters, 1986. The radiation extinction and diffusion were based on the scattering from arbitrarily inclined leaves (SAIL) model (Verhoef, 1984, 1985). Canopy clumping was taken into account in the model of radiation transfer by using a clumping factor which adjusts the leaf area used by the SAIL sub-model.

Canopy gross photosynthesis was calculated every half-hour according to Farquhar et al. (1980) and modified with a stomatal conductance model according to Ball et al. (1987). Leaf nitrogen effect on photosynthesis was taken into account assuming a linear relationship between the maximum carboxylation rate (V_{cmax}) and leaf nitrogen content per unit area (N_a) with a slope of α_{Na}. A fixed ratio (β) between V_{cmax} and the potential rate of electron flow (V_{jmax}) is used (Leuning, 1997).

All phenological events were calculated daily depending on day-degrees and day duration. Maintenance respiration (RM) depended on temperature and nitrogen content of various organs (Ryan, 1991a), while growth respiration (RG) depended on a construction cost fixed for an organ type (Dufrêne et al., 2005). Soil water balance and heterotrophic respiration (Parton et al., 1987) were also simulated.

After accounting for leaf growth and maintenance respiration the remaining carbon was allocated to the four other compartments (aboveground woody organs, reserve, coarse and fine roots). The growth of the different organs (GB$_{org}$) was a proportion (allocation coefficients) of the available carbon:

$$GB_{org} = \frac{AG_{org}}{CR_{org}}(A_{can} - RM - RG_{leaf} - GB_{leaf}) \tag{1}$$

where AG$_{org}$ is the allocation coefficient per organ type (the sum of the four coefficients is one), A_{can} the gross canopy photosynthesis, CR$_{org}$ the organ construction cost, RM the total maintenance respiration (all organs), RG$_{leaf}$ the leaf growth respiration and GB$_{leaf}$ the leaf growth. GB$_{leaf}$ is the product of growth in area and mass. The dynamics of leaf growth in area followed degree-day according to Dufrêne et al. (2005) and the dynamics of leaf mass per area depended on degree-day and total radiation sum as in Davi et al. (2008).

In the basic version of the model, AG$_{org}$ is a parameter either considered as constant for a species or calibrated with measurements for a site. The initial parameterization was done on two sites (see Dufrêne et al., 2005; Barbaroux, 2002) independent from the validation site (Fontainebleau Forest).

The values of allocation coefficients are given in Table 1 and the method of calculation is described by Barbaroux (2002). In the new version of the model, the allocation coefficients to roots and reserves were calculated using functional rules described below. In the two versions, the allocation coefficient to aboveground wood was the result, not calibrated with the growth measurements of aboveground wood (branches plus stem increment); consequently, the comparison between the measured and the simulated wood growth gave an evaluation of the model.

A complete description of the model is given by Dufrêne et al. (2005). The different sub-models were validated in 1997 in the Hesse site (Davi et al., 2005) by comparison with local (respiration chambers and branch bags) and integrated fluxes (eddy covariance measurements).

2.1.2. Improvement of carbon allocation to fine roots

The carbon allocation to fine roots strongly affects their surface area. Models describing the hydraulic architecture predicted the existence of a relationship between the surface areas of roots and leaves. We proposed an empirical model of carbon allocation based on hydraulic constraints. The allocation coefficient for fine roots (AG_{fr}) was calculated each day (t) from the ratio between theoretical biomass of fine roots which maintains the hydraulic balance in the soil-plant continuum (B_{th}) and current fine roots biomass (B_{fr}):

$$(AG_{fr})_{t+1} = (AG_{fr})_t \left(\frac{B_{th}}{(B_{fr})_t} \right) \tag{2}$$

B_{th} was calculated for each day as a function of leaf biomass (B_{lv}) and a proportionality factor (coef) accounting for total hydraulic conductivity, average height of trees and turnover rate of fine roots. This factor was calculated by inverted the equations given by Magnani et al. (2000):

$$TR_{max} = \frac{\Psi_{soil} - \Psi_{leaf} - Hg\rho_w}{R_{root} + R_{shoot}} \tag{3}$$

TR_{max} is the relationship between the surface areas of roots and leaves at maximum transpiration, Ψ_{soil} is water potential around fine roots, Ψ_{leaf} is water potential in leaves, H height, g is the gravitational constant, ρ_w is density of water and R_{root} and R_{shoot} are root and shoot resistances to water flux, respectively. It was thus possible to determine a relationship among the biomass of leaves, roots and sapwood. If a constant maximum transpiration was assumed, then taller trees (H in the Eq. (3)) require smaller resistances (R_{root} and R_{shoot}) to maintain the same water flux. To decrease R_{root} the root surface area can be increased. From Eq. (3), Magnani et al. (2000) deduced a relationship between coef and the various characteristics of a stand:

$$coef = \frac{1 + cH (TO_{sap}/TO_{fr})}{K_r R_{hyd} LMA} \tag{4}$$

with

$$c = \sqrt{\left(\frac{\rho_s K_r TO_{fr}}{K_s TO_{sap}} \right)} \tag{5}$$

where ρ_s is wood density, K_s is the hydraulic conductivity of sapwood, K_r is the hydraulic conductance of fine roots and TO_{fr} and TO_{sap} are turnover rates of fine roots and sapwood, respectively and R_{hyd}. The total hydraulic resistance Fine roots turn over is taken to 1 per year (Bauhus and Bartsch, 1996). This value measured for beech is higher than the average one found for temperate forest ecosystem of 0.65 (Gill and Jackson, 2000). Maximum transpiration (T_{Rmax}) was calculated by CASTANEA.

The allocation to coarse roots (from seedlings to mature trees) took into account the root/shoot ratio (RS), which started at 1.14 at 1 year and stabilized to RS_{min} after 20 years. For saplings, to reproduce a link between the coarse and fine roots, coef was adjusted proportionally to RS.

2.1.3. Improvement of carbon allocation to the reserves

Carbohydrate reserves (Rv) are immobilized in sapwood and roots to provide energy for the winter period (Ögren, 2000). In the case of deciduous species, new leaves require the use of this stored energy which causes a sharp decrease in carbohydrate concentration during budbreak and leaf growth (Barbaroux, 2002; Barbaroux et al., 2003). We developed and parameterized a new empirical allocation model. This simple model simulated dynamics of the allocation coefficient (AG_{Rv}) at the scale of days to years. It simulated an AG_{Rv} increase when the level of reserves was too low (force restore model). In other words, the sink strength of the reserves increased when the level of reserves decreased. However, the level of reserves cannot be decoupled from allocation to the stem (AG_w) and coarse roots (AG_{cr}). Barbaroux (2002) showed that the maximum reserve concentration in wood was close to a constant

Table 1 – Main species specific input parameters of CASTANEA

	Beech	Sessile oak
Slope of the dependency between V_{cmax} and leaf nitrogen density	20[a]	12.7[b]
Intercept of the dependency between V_{cmax} and leaf nitrogen density	0	50[b]
Ratio between V_{cmax} and V_{jmax}	2.2[a]	2.2[b]
Quantum yield	0.292[c]	0.292[c]
Slope of the Ball relationship	11.8[d]	11.8[d]
Temperature effect for respiration (Q_{10})	1.84[e]	1.84[e]
Root shoot after 20 ans (RS_{min})	0.2[f]	0.2[f]
Clumping factor	0.79[g]	0.79[g]
Critical state of forcing for budburst	450[h]	594[h]
In the basic version of the model		
Allocation to fines roots	0.22[i]	0.27[i]
Allocation to coarse roots	0.10[i]	0.08[i]
Allocation to reserves	0.18[i]	0.22[i]
Allocation to aboveground wood	0.50[i]	0.43[i]

On hemi-surface basis.
[a] Liozon et al. (2000).
[b] Medlyn and Jarvis (1999).
[c] Medlyn et al. (2002) and Ehleringer and Björkman (1977).
[d] Medlyn et al. (2001).
[e] Damesin et al. (2002).
[f] Korner (1994).
[g] Personnal data.
[h] Calibrated.
[i] Estimated in two sites independent from the "validation" site.

for a mature tree for a given species. AG_{Rv} was thus calculated from the concentration (Rv) and not from the reserves biomass (Brv). AG_{fr}, AG_{Rv} and AG_w were simulated according to following equations:

$$
\begin{aligned}
\text{If}(Rv_t > 0.05) \quad \text{then} \quad &
\begin{cases}
AG_w = \dfrac{1 - AG_{fr}}{1 + (RS + R\,(Rv_{opt}/Rv_t))} \\
AG_{cr} = RS \times AG_w \\
AG_{Rv} = AG_w R \dfrac{Rv_{th}}{Rv_t}
\end{cases} \\
\text{Else} \quad &
\begin{cases}
AG_{fr} = 0.05 \\
AG_{Rv} = 0.5 \\
AG_w = (1 - AG_{fr} - AG_{rv})/(1 + RS) \\
AG_{cr} = RS \times AG_w
\end{cases}
\end{aligned}
\tag{6}
$$

When reserves are too low, half of the carbon is allocated to the reserves to avoid tree death. The two parameters of this model describing allocation to reserves were the optimal concentration of reserves (Rv_{opt}) and the relationship between allocation to aboveground wood and to reserves (R).

2.1.4. A model predicting LAI variability between years

A model of LAI was developed for beech and oak. In the initial version of CASTANEA (Dufrêne et al., 2005), the maximum LAI for a year was a forced parameter depending on sites and years. This parameter was estimated either by in situ measurements (Davi et al., 2006b) or derived from remote sensing (Davi et al., 2006a; le Maire et al., 2006). In the current study the LAI was directly calculated from the reserve concentration. LAI can be broken down into two parameters: the average surface area per leaf (S_l) and the number of leaves covering a unit of ground surface area (N_l). In this study, we hypothesized that S_l was constant between years at our site, meaning that LAI varied only with N_l. Although some studies have found strong variation in S_l between years (Bussotti et al., 2000), we believe that this may be a sampling artefact. There is a large gradient in leaf area from top to bottom of the canopy and the common choice used in this kind of study is to sample only the upper third of the crown. However, there is still too much variability within the upper third to separate year effect and sampling effect.

The number of buds and leaf primordia in the buds determines N_l and these are set in late summer of the previous year. Bud mortality can also occur before budbreak of the current year. Consequently, the level of reserves just before budbreak is probably the best index integrating all the past conditions: carbon available during bud formation and during the period of leaf expansion. To express the relationship between Rv at the date of budbreak and N_l, a logistic curve was used:

$$
N_l = R_{\min\max} N_{\max} + \frac{(1 - R_{\min\max}) N_{\max}}{1 + (R_V/C_{LAI2})^{C_{LAI1}}}
\tag{7}
$$

where $N_{\max}$ is maximum number of leaves per square meter of ground area, $R_{\min\max}$ is the relationship between $N_{\max}$ and minimum number of leaves for a given species, and R_v is the reserves concentration at budbreak date. C_{LAI1} (negative) and C_{LAI2} are two calibration parameters of the logistic equation. Equations for sigmoid curves have been tested but gave poor

results (Davi, 2004). The thinning effect was simply accounted for by a proportional decrease in N_l.

2.1.5. Simulating height, diameter and mortality of trees

Simple empirical algorithms allowing simulation of stand density, average height and diameter were employed in the improved version of CASTANEA. The development of stand density depended on thinning and natural mortality due to competition.

Stems were removed using a thinning parameter (P_{thin}), which was either known at a given date or simulated according to forestry treatment. The proportion of stems removed was seldom equal to the proportion of biomass removed; therefore, a proportionality factor (β_{cut}), was used to calculate the proportion of biomass removed (P_{thinB}) for a given proportion of stems removed.

Mortality was estimated from quantity of reserves. CASTANEA simulates an average tree. To reproduce the proportion of dead trees, it was first necessary to distribute the level of reserves among trees. For this, we used a random variable from the normal distribution with a standard deviation of σ_{Rv}. A stem whose reserves (B_{rv}) became negative was then considered to be dead. σ_{Rv} was calculated as follows from level competition (S_{tc}) and a calibrated constant (β_{stc}):

$$
\sigma_{Rv} = \beta_{stc} S_{tc}
\tag{8}
$$

When there is more competition, the standard deviation increases and there would be more dead trees. S_{tc} was estimated from the diameter of the crown projection (λ_c) according to Bossel (1996):

$$
S_{tc} = \frac{n_s}{10000} \frac{\pi}{4} (\lambda_c D)^2
\tag{9}
$$

where D is average trunk diameter in cm and n_s is stem number per hectare.

Average tree height and diameter were calculated annually. The increment of aboveground woody biomass was simulated by CASTANEA (GB_w) and distributed between branches (P_{bch}) and trunks as a function of stand age (Le Dantec et al., 2000). Increases in diameter (R_d) and height (R_h) were calculated following the approach used in TREEDYN3 (Bossel, 1996; Peng et al., 2002):

2.2. The study site

The Fontainebleau forest is located southeast of Paris, France (48°25′N, 2°40′E, elevation 120 m). The dominant 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 (3.1 °C in January and 19.3 °C in July) and a mean precipitation of 750 mm. The forest is managed by the French National Forest Office (ONF). The predominately sandy soil is due to Stampian sandstone parent rock and windborne sand deposition. The windborne sand is composed of Stampian sand mixed with loam and clay. A sample of 20 stands dominated by *Q. petraea* and *F. sylvatica* was studied in detail (Table 2).

Table 2 – Site-specific parameters of 22 stands in Fontainebleau forest							
Stand	Dominant species	Leaf nitrogen content[a] (%)	LMA[a] (g_C m^{-2} leaves)	SEW[b] (mm)	$B_{aboveground}$ (g_C m^{-2} soil)	Age (1994)	Height (m)
164	Quercus	2.3	111	121	11,131	161	28
178	Quercus	2.41	113	178	14,544	181	30
180–181	Quercus	2.22	111	111	11,763	133	31
542–553	Quercus	2.6	108	98	17,560	199	39
566	Quercus	2.36	108	143	11,705	207	29
552–551	Quercus	2.47	94	93	12,939	163	37
676–666	Quercus	2.11	113	142	9,232	111	24
40	Quercus	2.05	108	88	7,528	88	23
687	Quercus	2.26	123	168	14,077	148	26
576	Quercus	2.26	117	189	14,496	188	32
555	Quercus	2.1	132	131	1,069	13	8.5
543	Quercus	2.52	112	157	2,707	17	11.5
678	Fagus	2.39	109	99	5,021	46	22.3
675	Fagus	2.33	115	112	6,514	48	21
80–82	Fagus	2.74	102	115	4,194	44	18
637	Fagus	2.29	97	126	11,876	79	31
639	Fagus	2.4	96	136	5,570	80	22.3
554	Fagus	2.26	90	101	13,628	131	31
174	Fagus	2.5	104	106	2,912	33	15
556	Fagus	2.8	106	133	3,494	29	14

[a] Leaf mass per area of sunlit leaves measured in 2002.
[b] Soil extractable water.

2.3. The model parameterization

2.3.1. Species-specific parameters
A complete parameterisation of the model is given by Dufrêne et al. (2005) for beech and by Davi et al. (2006c) for oak. The species-specific parameters are given in Table 1.

2.3.2. The site-specific parameters
The site-specific parameters are given in Table 2. All parameters varying spatially and required for the model parameterization are available for the 20 stands (le Maire et al., 2005; Davi et al., 2006b). During the period 1994-1999, LAI was estimated with the Plant Canopy Analyser (PCA LAI-2000) between June and mid-July using the three upper rings (Le Dantec et al., 2000). Stem diameter was measured during the winter of 1995-1996. Tree volume in each diameter class was determined by allometry according to Bouchon (1982) and converted to biomass using measurements of wood density. Aboveground woody biomass of the stand was then calculated from diameter distribution and tree biomass in each diameter class (Barbaroux, 2002). The biochemical and biophysical characteristics of leaves were determined in July 2002, using samples of 10 sun exposed and 10 shaded leaves on five trees per stand. Nitrogen content (N) and leaf mass per area (LMA) were then determined. Leaf area was measured using a leaf area meter (Delta-T Area meter). The leaves were dried (60 °C) and weighted to obtain leaf dry mass and ground into powder. An element analyser (Thermo-Quest NCS 2500, France) was used to obtain nitrogen and carbon content. The soil water content was estimated using the French National Forest Office soil database for 1995. From soil depth, and soil texture, the Soil Water Reserve (SWR) was estimated according to Saxton et al. (1986). The parameters are summarized in Table 2 and Table 6 for LAI.

2.3.3. parameterization of allocation model to fine roots
We developed allometric equations for beech and oak using existing parameters (Magnani et al., 2000; Kowalik et al., 1997; Nardini and Pitt, 1999; Lemoine et al., 2002; Barbaroux, 2002; Damesin, 1996; Bauhus and Bartsch, 1996) in equations from Scots pine (Magnani et al., 2000). The complete parameterization is given in Table 3 and a sensitivity analysis for tree height is presented for oak and beech in Fig. 1. According to this model, beech allocates less to fine roots than oak when trees are smaller and more when trees are taller.

2.3.4. parameterization of model for allocation to reserves
The two parameters of the model for allocation to reserves Rv_{opt} and R were estimated from measurements of reserves for beech

Table 3 – Constants used for the simulation of the carbon allocation to the fines roots			
Symbol	Unit	*Fagus sylvatica* L.	*Quercus petraea*
ψ_{crit}	Mpa	−2.2[a]	−1.85[b]
ρ_s	kg m^{-3}	550[c]	660[c]
K_r	gH$_2$O MPa^{-1} m^{-2} s^{-1} g$_C^{-1}$	4.7E−6[d]	6.2E−7[e]
K_s	gH$_2$O MPa^{-1} m^{-2} s^{-1} m^{-1}	5.6E−5[d]	1.0E−3[e]
TO$_{fine roots}$	an^{-1}	1[f]	1[f]
TO$_{sapwood}$	an^{-1}	0.025[g]	0.025[g]

[a] Lemoine et al. (2002).
[b] Damesin (1996).
[c] Barbaroux (2002).
[d] Kowalik et al. (1997).
[e] Nardini and Pitt (1999).
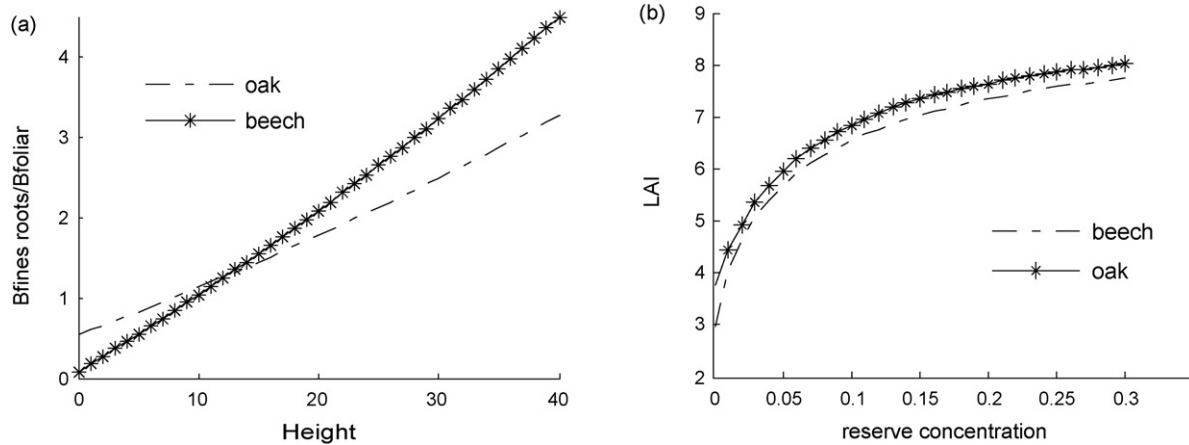[f] Bauhus and Bartsch (1996).
[g] Magnani et al. (2000).

Fig. 1 – (a) Simulation of the ratio of fine roots biomass to foliar biomass according to height and (b) simulation of LAI according to level of reserves.

trees in Hesse, Germany and oaks in Champenoux, France (Barbaroux et al., 2003). The estimates of Rv_{opt} resulted directly from measurements. R was estimated by inverting the CASTANEA model for the two experimental sites where the model was evaluated. The parameters are given Table 4. Sessile oak allocates more carbon to reserves than beech. This may explain its capacity for early growth of wood before budbreak (Barbaroux, 2002).

2.3.5. parameterization of the LAI model

First, we tested whether the spatial and temporal variation in LAI was due primarily to the variation in N_l using the Fontainebleau data. The data for S_l from eight sites (four beech and four oak stands) showed little variation between 2000 and 2001 (slope 1.03, $r^2 > 0.99$). Also, on 22 sites in 2002, we measured S_l and LAI, and calculated N_l according to: $N_1 = LAI/S_l$ showed that more than 70% of the variability in LAI was explained by variation in N_l (Fig. 2). These measurements were used to estimate the relationship between minimum and maximum number of leaves (R_{minmax}). Lastly, the two parameters of the logistic equation (Eq. (7)) were calibrated (Table 5) and a sensitivity analysis of the reserve concentration is presented for oak and beech (Fig. 1b).

3. Results

3.1. Growth of aboveground biomass

First, the model for allocation to reserves and fine roots was evaluated without LAI modelling. When allocation coefficients

were constant, the simulations did not reproduce the growth variations between sites (Fig. 3b). Growth was systematically over-estimated (Fig. 3a and b), though more than 70% of variability between years was reproduced. The new version of the allocation model improved the capacity of the model to reproduce growth variation between sites (Fig. 3d), except for two stands. In these two stands (40 and 555), growth simulation diverged even more from measurements than in the simple version of the allocation model. In stand 40, lower LAI caused lower carbon allocation to the fine roots in simulations that was probably underestimated. In stand 555, the low stand density (433 stems ha^{-1} for 88 years old) probably explained the low growth measurements. The model did not explicitly take into account the effect of stand density on growth. Therefore, it probably over-estimated growth when stand density was abnormally low due to forest management. On the 18 other stands, results were more conclusive. The new model reproduced 41% of the variability between sites. It did not overestimate the average growth (Fig. 3e) but it modified the dynamics a little between years. The reserves dynamics was much more stable with the new version (Fig. 3f) and the productivity decline with age was

Table 4 – Allocation parameters to the reserves			
	Symbol	Sessile oak	Beech
Reserves concentrations[1]	[Reserves]th	0.3	0.2
Relationship between allocation to reserve and aboveground wood	R	0.51	0.35

[1]Concentration related to the aboveground live woody biomass.
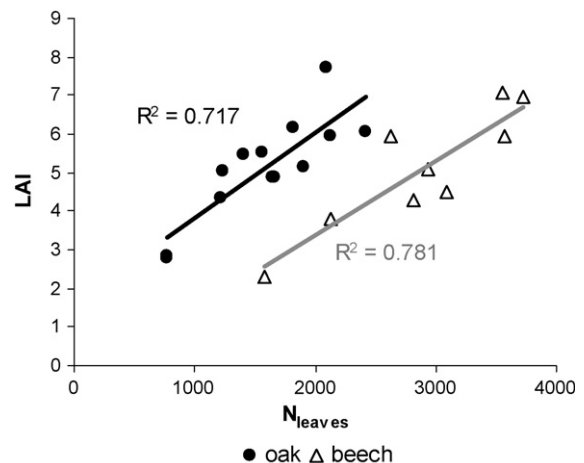

Fig. 2 – Relationship between number of leaves (N_{leaves}) and leaf area index (LAI) for 22 stands in Fontainebleau.
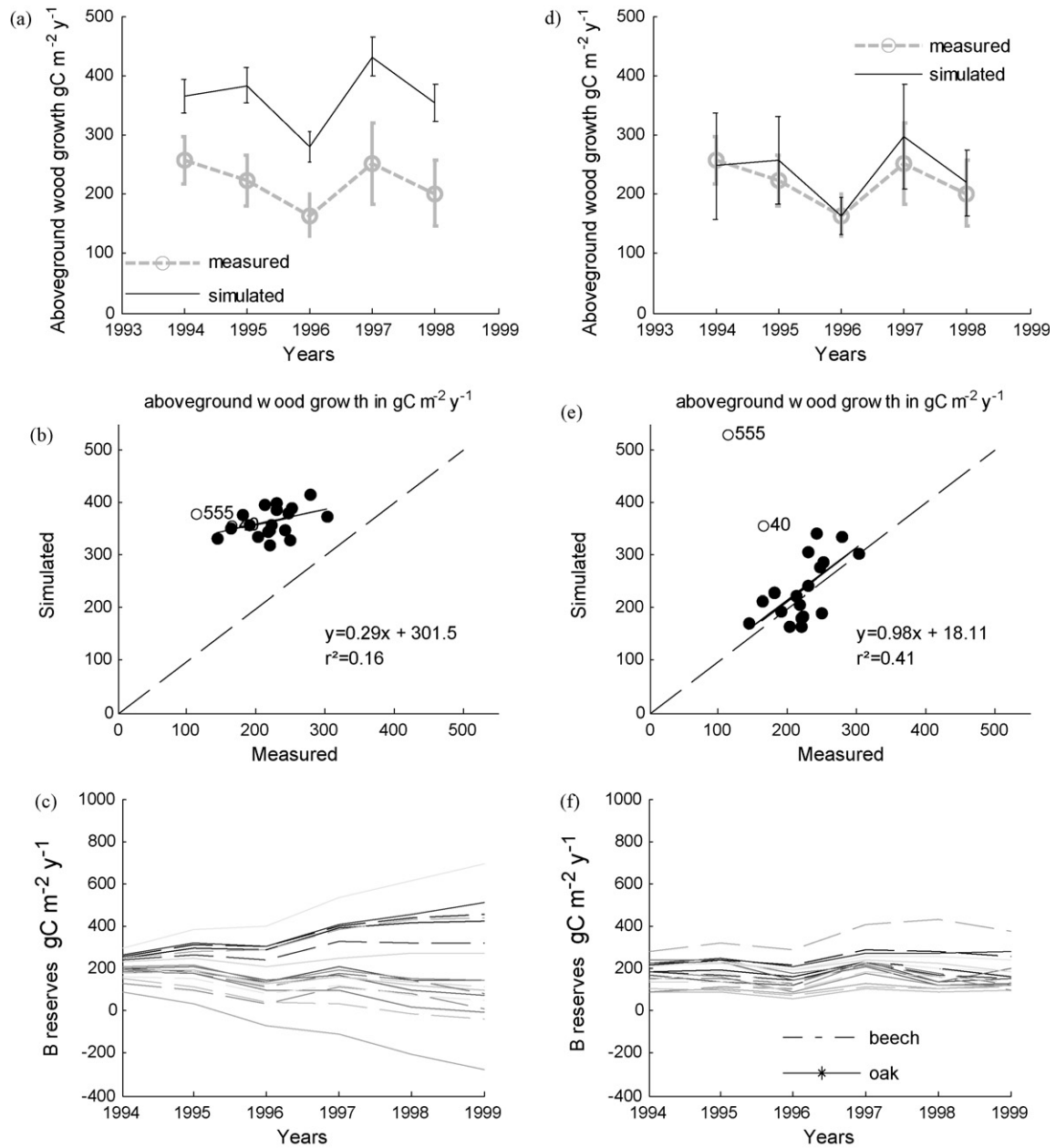
Fig. 3 – Evaluation of the allocation model in Fontainebleau. *Variability of aboveground growth between years*: average growth of 18 stands (without stand 40 and 555) measured and simulated with constant (a) or variable allocation (d). *Variability of aboveground growth between sites*: average growth of each stand between 1994 and 1999, measured and simulated with constant (b) or variable allocation (e). *Biomass of reserves* for each site and each year simulated with constant (c) or variable allocation (f).

Table 5 – Parameters used for leaf area index (LAI) simulation

	Symbol	Sessile oak	Beech
Average leaf area (cm^2)	S_{leaves}	33	18
Maximum leaf number per ground unit (N m$_{ground}^{-2}$)	N_{max}	2800	5000
Minimum leaf number per ground unit (N m$_{ground}^{-2}$)	N_{min}	900	2100
Relationship between N_{max} and N_{min}	R_{minmax}	0.32	0.42
Logistic parameter	C_{LAI1}	−0.8	−1
Logistic parameter	C_{LAI2}	0.07	0.07

Table 6 – Leaf Area Index of 22 stands in Fontainebleau from 1994 to 1999						
Stand	LAI					
	1994	1995	1996	1997	1998	1999
164	6.39	6.28	6.79	5.72	6.45	6.33[a]
178	5.61	5.45	5.54	5.65	5.88	5.63[a]
180–181	6.27	6.50	6.85	5.50	7.08	6.67
542–553	4.97	5.39	5.57	4.98	6.70	6.58
566	6.61[a]	6.55	7.05	5.87	6.99	6.61[a]
552–551	6.11[a]	6.71	6.02	5.32	6.37	6.11[a]
676–666	6.07	6.64	7.11	6.13	7.02	6.44[a]
40	3.66[a]	3.81	3.52	2.90	2.84	2.87[a]
687	6.21	6.85	7.02	5.84	6.73	6.70
576	5.79[a]	4.88	5.88	5.40	6.10	5.79[a]
555	3.58[a]	2.05	4.31	3.01	3.70	3.30
543	6.80[a]	6.85	8.04	6.39	5.92	6.80[a]
678	3.21	3.90	4.69	5.04	6.23	3.51
675	3.58	4.29	4.94	5.49	6.42	4.30
80–82	5.21	6.03	6.49	5.56	6.67	6.40[a]
637	5.00	4.18	4.95	4.60	5.56	5.60
639	5.63[a]	5.33	6.10	5.52	5.59	5.63[a]
554	4.08	4.12	3.80	3.49	3.45	3.79[a]
174	7.96	7.72	7.83	6.20	6.62	7.84[a]
556	8.06	7.21	7.61	6.12	6.58	6.40[a]

[a] LAI not measured for this year in this stand, the given LAI is the average LAI measured in this stand between 1994 and 1999 by excluding the years of cutting.

reproduced (Fig. 4). Finally it is interesting to note that simulated gross primary production did not explain the variation in measured woody growth ($r = -0.27$). The correlation between simulated GPP and measured woody growth was even negative!

3.2. LAI simulation

The model reproduced 70% of LAI variation between sites (Fig. 5a) if stands 40 and 555 were excluded (but with a positive bias of 0.02). The variation between years was well simulated (Fig. 5b): note the effect of water stress in 1996 leading to a
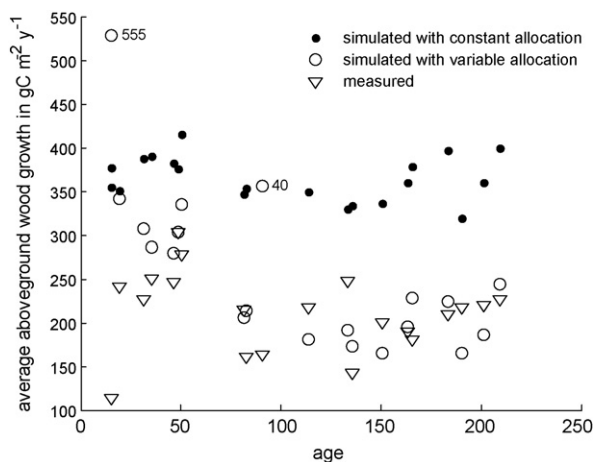

Fig. 4 – Average growth (1994–1998) of 20 stands, measured or simulated with and without age effect on carbon allocation.

decline in measured and simulated LAI the following year (1997).

4. Discussion

4.1. Why level of growth is better reproduced?

As allocation to aboveground biomass is the result of the allocation schema, not calibrated with the growth measurements, the comparison between the measured and the simulated wood growth gave an evaluation of the model. The new version of the model first improved the simulation of the level of growth. In the old version, we apply allocation coefficient calibrated on two (one beech and one oak) productive young forests, on 20 older and poorest stands in Fontainebleau. By doing this, we strongly overestimated the average growth. By only changing carbon allocation in function of age, height and aboveground biomass, the model fits better the measurements. In Fontainebleau, the simulated fine roots biomass is in average 228 for beech and 308 g_C m^{-2} year^{-1} for oak, although it was 164 for beech and 288 g_C m^{-2} year^{-1} for oak in the calibration sites. In Fontainebleau, trees are older and higher and should invest more carbon in fine roots. Moreover, as aboveground biomass is also higher, both autotrophic respiration and consequently carbon allocated to reserves are higher of 12% in Fontainebleau than in the calibration sites. To conclude, taking into account photosynthesis and respiration modifications, when changing of simulation sites, is not enough to correctly reproduce the level of growth: variations in allocation need also to be included.

4.2. What are the causes of growth variability between sites?

In the new version, we also improved the capacity of the model to reproduce growth variability between stands. In Fontainebleau, parameters controlling photosynthesis through fertility vary little (Table 2): For each species, the coefficient of variation (CV) between stands of N and LMA is ranged between 7 and 8%. Soil extractable water acting on photosynthesis through water stress varies more (CV$_{beech}$ = 12% and CV$_{oak}$ = 25%). CV of LAI is in average 22% for both species. But, the more variable input parameters are the height (CV = 32%), the age (CV = 52%), and the aboveground biomass (CV = 53%). Consequently, the variability between stands of main simulated fluxes is weak: 15% (oak) and 6% (beech) for autotrophic respiration, 8% (oak) and 10% (beech) for transpiration and 7% for photosynthesis (both species). The variability of simulated allocation to roots (27 and 7%, respectively, for oak and beech) and reserves (11 and 10%, respectively, for oak and beech) is higher. To conclude, the old version of the model accounted for only the variability between of transpiration, photosynthesis and respiration, although the new version include the variability of allocation, what explains the improved correlation coefficient between measurements and simulations.

Age, aboveground biomass and tree height vary between stands as much for beech as for oak. But the simulated growth is more variable for oak because allocation to reserves and fine
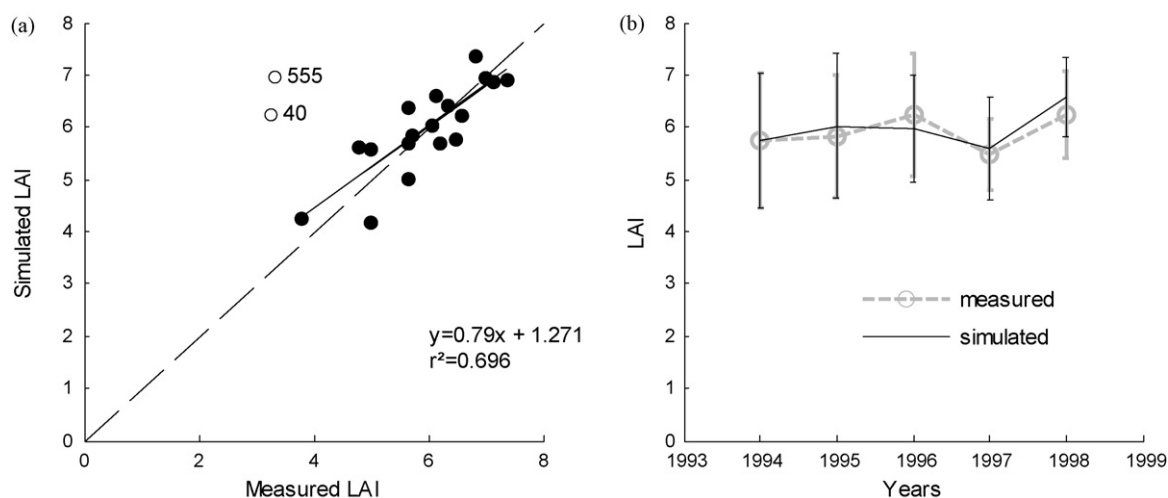
Fig. 5 – Evaluation of the LAI sub-model. (a) *LAI variability between sites*: **the average of each stand between 1994 and 1999 measured and simulated and (b)** *LAI variability between years*: **the average for each year of 18 stands (without stand 40 and 555).**

roots are more sensitive respectively to reserves and height changes.

4.3. Allocation to aboveground biomass

The use of an allocation scheme which accounts for the variability in carbon allocation to fine roots and reserves improved the simulation of wood growth increments. These preliminary results are encouraging, knowing that the model does not consider many factors limiting to growth: the deficiency of phosphorus or potassium, effect of water stress acting directly on cell division and elongation or on turnover of fine roots, effects of hydromorphy or of forest management practices. This study demonstrated the importance of carbon allocation in explaining growth variability between sites. As stated by Magnani et al. (2000), the variations of carbon allocation partly explain the productivity decline with age. Nevertheless, it is possible that part of the growth variability was reproduced without targeting the right causality factors (Mäkelä and Valentine, 2001). Indeed, it is conceivable that the simulated variability of allocation to fine roots and reserves was only correlated with the true causality factor. To check, the real variability of allocation has to be measured. This can be carried out by direct measurements like fine roots biomass. In addition, the variability of simulated photosynthesis was not evaluated at this site. Measurements of stomatal conductance or foliar photosynthesis on stands along gradients of age or fertility would provide an independent check to see if the spatial variability of GPP really did not explain the variability of measured growth. Finally, using and validating the algorithms simulating mortality processes constitutes one of the main research orientations in the field (Martinez-Vilalta et al., 2002).

4.4. Productivity decline with age

The decrease in productivity with age is well documented (Sprugel, 1985; Gower et al., 1996; Ryan et al., 1997) but little is known of the processes involved and these have only recently begun to be quantified. The age effect can be due to multiple causes. Four main causes are possible: increase in tree height, increase in the proportion of living wood, decline of soil fertility, and increase in carbon allocation to reproduction.

4.4.1. A decline in input carbon (photosynthesis)
The decrease in stomatal conductance and consequently of photosynthesis is a possible mechanism for a decline in photosynthesis that was not taken into account in our approach. To prevent embolism, the plant can close the stomata. A decrease in stomatal conductance with tree age has been shown for many species with foliar or sapflow measurements (see Niinemets, 2002 for a synthesis). But, in many studies, the decrease in stomatal conductance does not completely explain the decrease in photosynthesis (Day et al., 2001; Niinemets, 2002).

A decline in photosynthesis can also be due to immobilization of nutrients in wood that reduces litter quality (C/N increase) and rate of decomposition (Murty et al., 1996). Accounting for the reduction in nutrient availability was not possible with CASTANEA, since the model did not simulate the cycling of nitrogen or other minerals (phosphorus and potassium). A nitrogen deficiency was not very probable, considering the high foliar nitrogen measured at the study site (Table 2). However, phosphorus and potassium measurements indicated the existence of nutritional imbalances (Barbaroux, 2002). They can be potentially limiting factors, but no negative tendency was found between phosphorus or potassium and tree age.

LAI can also decrease with age due to lack of reserves or hydraulic constraints (Shinozaki et al., 1964). Moreover, when canopy openness occurs at old age, the stand density is low and LAI must decrease in response. Consequently, the stand GPP might decrease.

4.4.2. A decline in available carbon for growth by increase in respiration
The increase of live biomass can cause an increase in maintenance respiration and thus a reduction in growth

may occur. In CASTANEA, maintenance respiration depends on living biomass. This is a function of the proportion of total biomass to living biomass ($B_{alive} = P_{live}B_w$). P_{live} decreased with age and the effect was stronger in branches than in the trunk. Consequently, the effect of age on maintenance respiration depended on the changes in total biomass, P_{alive}, and on the proportion of branches. Using the relationships implemented in CASTANEA (Barbaroux, 2002), the effect of biomass increase on respiration was found to be negligible (Davi, 2004). The studies of Ryan (1991b) and Ryan and Waring (1992) reached a similar conclusion to this study, since between the old and the young trees, they found a respiration increase of 5% but a productivity decrease of 40%.

4.4.3. A decrease in wood growth caused by re-allocation of carbon to roots or reproduction

Allocation of carbon to fine roots according to hydraulic constraints (due to the increase in height), caused an age effect as described by Magnani et al. (2000). In our approach, the hydraulic conductance was constant, but it has been shown to increase with an increase in sapwood surface area. This phenomenon was shown by Barnard and Ryan, 2003 who compared two plantations of *Eucalyptus saligna* of various age. Delzon et al. (2004), found the same result on a chronosequence of *Pinus pinaster*. Nevertheless, in their case, the increase in sapwood surface area with leaf area was not enough to compensate for the increase in height. They also observed a decrease in stomatal conductance.

The investment in reproduction (seed production) consumes a significant part of photosynthate. For example, biomass of fructification in beech can reach 217 g_{DM} m^{-2} (Nielsen, 1977). However, years when fructification is important are rare and the effect on wood growth is inevitably discontinuous, which is not the case for the age effect.

The age effect on aboveground woody biomass is caused by all of these factors, but vary in importance according to species and ecosystem. In this study, we showed that the variation in carbon allocation was probably the main factor contributing to variation in above ground woody biomass in the Fontainebleau forest. In a previous study, Zaehle et al. (2006) found the same result. With our study, we also confirmed that carbon allocation might be a direct cause of the age effect. We showed that changes in carbon allocation can be caused by the increase in tree height, which results in a greater allocation to roots to maintain the same hydraulic conductance.

4.5. LAI simulation

Leaf number is partly defined the previous year during the bud production. Bud mortality can occur if the conditions at budbreak are unfavourable (dryness or low level of reserve), which subsequently results in a reduction in total leaf surface area. Therefore, the LAI of the current year depends not only on the "environmental" conditions of the current year but also of the previous year, when the buds were set and the reserves were filled. In our allocation model, the reserves (Rv) was an efficient variable, which integrated the carbon and water budget across several years. Indeed, if reserve production was low during a year (strong water stress or little radiation), the concentration in reserves was lower at the end of the year. In addition, the

hydraulic constraints due to tree height influenced the Rv in our allocation model, since the allocation to fine roots increased with tree height and limited allocation to wood and reserves. This explained the decrease in the simulated LAI with tree age. To conclude, this model linking Rv and LAI reproduced three well known sources of spatial and temporal LAI variation: the decline in LAI in a year following one with strong water stress (Le Dantec et al., 2000), the LAI decline with average tree age and the LAI decline following a cut.

5.   Conclusion and perspective

To couple process-based and forestry models, we proposed and evaluated some simple algorithms to simulate carbon allocation and leaf area index. By comparison of two versions of the model (with constant or variable coefficients of allocation), we showed that simulation of allocation process was necessary if one wants to reproduce and understand the observed variability of wood production. To improve the model, we must explore three points: the functioning of stomatal conductance and its decline with age, effects of forestry practices on carbon allocation and reproduction cost.

Simulation of LAI appears to be possible using a link between LAI and a variable that integrates several factors: the reserves level. The reserves are also the result of the carbon allocation process. Consequently, the allocation model acts indirectly on LAI. On the other hand, LAI controls photosynthesis and foliar respiration. We can conclude that our model linked the simulation of carbon allocation and LAI, in a way that closely resembles reality. The perspectives to improve the LAI model is to better account for the competition and thinning effects, by making an explicit link between LAI and stand density.

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