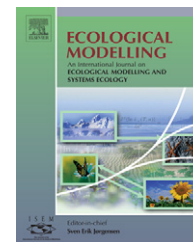


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/ecolmodel

Modelling leaf mass per area in forest canopy as affected by prevailing radiation conditions

H. Davi^{a,e,*}, C. Barbaroux^c, E. Dufrière^a, C. François^a, P. Montpied^b,
N. Bréda^b, F. Badeck^d

^a Laboratoire Ecologie, Systématique et Evolution (ESE), CNRS & Université Paris Sud, Bât 362, 91405 Orsay, France

^b UMR INRA-UHP Ecologie et Ecophysiologie forestières, F-54280 Champenoux, France

^c Laboratoire de Biologie des Ligneux et des Grandes Cultures, UPRES EA 1207, UFR-Faculté des Sciences, Université d'Orléans, rue de Chartres, BP 6759, 45067 Orléans Cedex 02, France

^d Potsdam Institute for Climate Impact Research (PIK), PF 60 12 03, 14412 Potsdam, Germany

^e INRA-UR629, Recherches Forestières Méditerranéennes, Domaine Saint Paul, Site Agroparc, 84914 Avignon Cedex 9, France

ARTICLE INFO

Article history:

Received 22 August 2006

Received in revised form

18 August 2007

Accepted 21 September 2007

Published on line 19 November 2007

Keywords:

Leaf mass per area

Photosynthetically active radiation

Modelling

Carbon

Fagus sylvatica L.

Quercus petraea (Matt.) Liebl.

Quercus ilex L.

ABSTRACT

Leaf mass per area (LMA) is a key leaf trait, which conditions the assessment of carbon balance and the adaptation of the species to their environment. LMA decreases exponentially within the canopy at a lower rate coefficient (k_{LMA}) than the extinction coefficient (k_{PAR}) of photosynthetically active radiation (PAR); consequently the canopy is not fully optimized for the carbon balance. A new algorithm to simulate LMA in forest canopies is developed. The algorithm is based on a relationship between LMA of leaves at a given canopy depth and PAR, that they absorb, during leaf growth. The LMA sub-model is then tested against independent experimental data to demonstrate its validity to assess (i) the LMA vertical distribution inside the canopy, (ii) its evolution during the season and (iii) the variability observed between sites, years and species. Then, the LMA sub-model is coupled with a process-based model simulating carbon, water and energy balances in forest ecosystem. The coupled model is applied to a sensitive analysis for a case study in a beech forest.

© 2007 Elsevier B.V. All rights reserved.

1. Introduction

Leaf mass per area (LMA) is defined as the ratio between leaf mass and leaf area; it is the inverse of the specific leaf area (SLA). LMA strongly conditions leaf photosynthesis and carbon uptake by plant canopies. For that reason, LMA is a key param-

eter of process-based models simulating plant growth (Bertin and Gary, 1998; Gracia et al., 1999; Wirtz, 2000; Dufrière et al., 2005; Davi et al., 2006). Moreover, it is a main leaf trait that characterizes the species adaptation to environmental conditions and its ecophysiological properties (Castro-Díez et al., 2000; Green et al., 2003).

* Corresponding author. Present address: INRA-UR629, Recherches Forestières Méditerranéennes, Domaine Saint Paul, Site Agroparc, 84914 Avignon Cedex 9, France. Tel.: +33 4 32 72 29 99; fax: +33 4 32 72 29 02.

E-mail addresses: hendrik.davi@avignon.inra.fr (H. Davi), cbarbaro@univ-orleans.fr (C. Barbaroux), eric.dufriere@ese.u-psud.fr (E. Dufrière), christophe.francois@ese.u-psud.fr (C. François), montpied@nancy.inra.fr (P. Montpied), breda@nancy.inra.fr (N. Bréda), badeck@pik-potsdam.de (F. Badeck).

0304-3800/\$ – see front matter © 2007 Elsevier B.V. All rights reserved.

doi:10.1016/j.ecolmodel.2007.09.012

1.1. LMA profile inside a canopy

Plants grown in high light generally have thick leaves with high LMA (Björkman, 1981) caused by extra layers of palisade mesophyll or longer palisade cells (Hanson, 1917). Light and LMA decrease exponentially within the canopy. Field (1983) showed that for a maximal carbon gain by a canopy, the nitrogen distribution per surface area ($N_a = LMA \times N_m$) within the canopy must exactly follow the distribution of light. The relative acclimation of leaves to the irradiance can be taken into account through LMA, because within the forest canopy, the nitrogen content (N_m expressed per mass unit) is often found constant (Jayasekera and Schleser, 1988; Evans and Poorter, 2001) or showing a slight increase from top to bottom (Niinemets, 1995). But this acclimation is not fully optimized (Gutschick and Wiegand, 1996; Warren and Adams, 2001; Meir et al., 2002; Kull, 2002). While the light shows an exponential decrease within the canopy with a coefficient ranging between 0.6 and 0.7, the LMA acclimates with a smaller rate ranging between 0.14 and 0.20. In other words, either sun leaves are too thin or shade leaves too thick to allow a full optimization of the carbon gain.

1.2. Variations of LMA between site and species

Interspecific variation in LMA has been described for a wide range of both herbaceous and trees species. LMA is an important determinant of interspecific variation in relative growth rate (Lambers and Poorter, 1992; Garnier, 1992) and correlates with a suite of other traits (Poorter and Evans, 1998; Wright et al., 2004, 2005). These variations can be explained in terms of (i) drought adaptation since high LMA increases the water use efficiency (WUE) or (ii) trade off between cost and leaf span (Chabot and Hicks, 1982); the evergreen species having generally higher LMA (Reich et al., 1997).

1.3. Why and how simulated maximal LMA during a year and its dynamics?

Many complex models in ecology require an estimation of leaf mass per area to simulate carbon or water exchange in canopies and soil or to model competition between different types of plants. In the literature many models that require LMA assume that this variable is constant inside a species or a functional group (Friend et al., 1997; King, 2005) or is forced by measurements (Simeoni et al., 2000; Dufrêne et al., 2005). Recent studies have shown that using an average value of LMA could potentially have a strong impact on NPP (Vose and Bolstad, 1999; Davi et al., 2006).

Some models simulate the leaf mass or leaf mass per area using different methods:

- (1) Some object-oriented models simulate development of the phytomers, whose elongation depends on temperature, and is not influenced by the current assimilate supply (Groot and Lantinga, 2004). This architectural approach is too time-consuming to be used in complex ecosystem models acting at stand or regional level.

- (2) Other models deduce leaf mass from the carbon budget simulated by a process-based model using allocation rules (Bossel, 1996; Kätterer et al., 1997; Running and Coughlan, 1998; Gracia et al., 1999). This method presents two major problems: (i) if the carbon budget depends of LMA dynamics and if LMA depends in return of carbon budget, the model can show strong drifts. (ii) When leaf unfolding occurs, during more than a week, the tree uses not assimilation from leaves, but from reserves. Consequently, a strict relationship between assimilation leaf growth, is false.
- (3) One other solution consists in using models (Wirtz, 2000) under the hypothesis of an optimal distribution of leaf traits. They simulate not only the LMA profiles but also the nitrogen allocation between chlorophyll and RUBISCO pools (i.e. investment in light absorption versus carboxylation). This solution assumes a strong hypothesis (optimal distribution), not reported by the measurements.
- (4) Some authors use empirical decrease of LMA with increasing irradiance (Niinemets and Kull, 1995; Niinemets et al., 2004), to deduce relationships between incident irradiance during growth and LMA (Niinemets, 1995). Without drought, the leaf expansion can be determined by irradiance by the means of various mechanisms: direct effect of the light (Andersson and Aro, 1997), phytochromes (Rousseau et al., 1996; Van Volkenburgh, 1999), or cytokinins transported in the transpiration stream (Pons et al., 2001). Since foliar carbohydrates are correlated with cell division (Chapin, 1991; Van Volkenburgh, 1999), they could also be a mediator of leaf acclimation (Niinemets, 1999). In all cases, the sum of the global radiation absorbed by the leaf during its growth is probably an efficient way to simulate the LMA.

Many of these models simulate only leaf mass growth, other simulate the LMA at maturity but not the dynamics. No model simulates simply directly LMA, both growth and value at maturity with the same algorithm. The main objective of this paper is to propose and to test a generic algorithm, which depends not linearly on the radiation interception, to simulate LMA profile inside the canopy, its seasonal dynamics and its variability between sites and years. Secondly, a sensitive analysis of the model is done.

2. Material and methods

2.1. Study sites

The sites used in this work are briefly described in Table 1. Three sites characterize a climatic gradient from Eastern to Western Europe covering the distribution area of beech (*Fagus sylvatica* L.): Solling in Germany, Hesse located in eastern France, Fougères located in western France. Two additional sites were used to test the models general applicability to other species: Champenoux for sessile oak (*Quercus petraea* (Matt.) Liebl.) in Eastern France and Puéchabon for holm oak (*Quercus ilex* L.) in South-Eastern France.

Table 1 – Description of the study sites used for the LMA sub-model parameterization and evaluation

	Hesse	Fougères	Solling	Champenoux	Puéchabon
Land	France	France	Germany	France	France
Latitude	48°40'N	48°67'N	51°82'N	48°44'N	43°44'N
Longitude	7°05'E	1°40'W	9°47'E	6°14'E	3°35'E
Altitude	300 m		500 m	237 m	270 m
Mean annual precipitations	820 mm	900 mm	1048 mm	744 mm	883 mm
Mean annual temperature	9.2 °C	12.9 °C	6.8 °C	9.2 °C	13.58 °C
Species	<i>Fagus sylvatica</i> L.	<i>Fagus sylvatica</i> L.	<i>Fagus sylvatica</i> L.	<i>Quercus petraea</i> (Matt.) Liebl.	<i>Quercus ilex</i> L.
Phenology type	Deciduous	Deciduous	Deciduous	Deciduous	Evergreen
Average LAI	6.5	8.0	5.4	6.0	2.3
Stand age	30	30	135–140	45	58
Density stem (ha ⁻¹)	3482	4260	250	2553	8500
Soil	Luvisol	Alocrisol luvisol	Cambisol	Luvisol	Calcareous fersiallitic
References	Granier et al. (2000)	Lebret et al. (2001)	Schulte (1993)	Bréda et al. (1995)	Hoff et al. (2002)

2.2. Measurements

In Hesse, Fougères, Champenoux and Puéchabon, vertical profiles of photosynthetically active radiation (PAR), of leaf area index (LAI) and of LMA were measured for forest canopy on towers every half meter (in Puéchabon) or meter (for the other sites). Vertical profiles of PAR were measured for eight orientations around the scaffolding, using Li191-SA (Li-Cor, Lincoln, NE, USA) sensor or Sun Scan Canopy Analysis System (Delta-T Device, Cambridge, England). Vertical profiles of LAI were measured for the same orientations, using PCA-LAI2000 (Li-Cor) with three rings (Welles and Norman, 1991; Dufrêne and Bréda, 1995; Olthof and King, 2000). Note that for each height, there not in all cases measurements for all the orientations could be taken since for a given height sometimes there was no branch for a given orientation. For each height and each orientation, one sample of 10 leaves was taken to estimate leaf nitrogen content and LMA: their surfaces were measured and then the leaves were dried (48 h, 65 °C) and weighted to obtain leaf dry mass. Grounded leaves were used to estimate the nitrogen content with an elementary analyser. In Solling, LAI and LMA only of sun and shade leaves were measured from 1986 to 1988 (see Schulte, 1993 for more details).

2.3. The process-based model

CASTANEA is a model simulating the carbon, water and energy balances in forest stands. Tree structure is represented by a combination of five functional compartments: leaves, stems, branches, coarse and fine roots. A reserve compartment is also represented but not physically located in the model.

The canopy is assumed to be horizontally homogeneous and vertically subdivided into a variable number of layers (i.e. multi-layer canopy model). Each layer contains the same amount of leaf area (typically less than 0.1 m² m⁻²). For each layer, three different radiative balances are calculated, in the PAR [400–700 nm], in the global radiation [400–2500 nm], and in the thermal infrared. Incident light is split into direct and sky diffuse radiation using equations given by Spitters

(1986). In the thermal infrared, the diffuse atmospheric radiation is computed from air temperature according to Idso (1981). The radiation extinction and diffusion are based on the SAIL model (Verhoef, 1984, 1985). In the thermal infrared, the radiation extinction is based on Beer's Law and the diffuse atmospheric radiation is computed from air temperature according to Idso (1981). The canopy clumping is taken into account using a clumping factor (Davi et al., 2006).

Half-hourly gross photosynthesis of canopy is calculated following Farquhar et al. (1980) coupled with a stomata conductance model of Ball et al. (1987). Leaf nitrogen effect on photosynthesis is taken into account assuming a linear relationship between the maximal carboxylation rate (V_{cmax}) and leaf nitrogen content per unit area (N_a), whose slope is α_{Na} . A fixed ratio (β) between V_{cmax} and the potential rate of electron transport (J_{max}) is used (Leuning, 1997). Because leaf nitrogen concentration (per mass) $N_{mleaves}$ ($g_N g_{DM}^{-1}$) is assumed to be constant inside the canopy, N_a ($g_N m_{leaf}^{-2}$) is calculated for each layer (L) directly from LMA profile (LMA_L):

$$N_{aL} = LMA_L N_{mleaves} \quad (1)$$

Photosynthesis is calculated for each layer, on sunlit (leaf area intercepting diffuse and direct PAR) and shaded (leaf area intercepting diffuse PAR only) foliage separately.

All phenological events and growth are calculated with a daily time-step depending on degrees-days and day duration. Maintenance respiration depends on temperature and nitrogen content of various organs (Ryan, 1991), while growth respiration depends on fixed construction cost depending on the organ type (Dufrêne et al., 2005). Water balance (Dufrêne et al., 2005) and heterotrophic respiration (Parton et al., 1987) are also estimated. A complete description of the model is given in Dufrêne et al. (2005) and 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 techniques measurements). The complete parameterization of the model is given in Dufrêne et al. (2005).

2.4. LMA algorithm

The duration of the leaf growth (leaves formation in the canopy and leaves expansion) was assumed to be dependant on degree-days, while LMA is directly a function of the absorbed PAR. As other phenological events simulated in the CASTANEA model, the LMA growth is calculated with a daily time-step. The phenological events (budburst, full leaf area development, full leaf maturity, start of leaf yellowing, complete canopy yellowing) depend on degree-days and daylength. The complete leaf maturation is achieved, when the temperature sum for leaf mass growth (S_{frCLMA}) reaches the critical value F_{critLMA} (Eq. (2)):

$$S_{\text{frCLMA}} = \sum_{D_{\text{BB}}}^{D_{\text{LMAmax}}} T \quad (2)$$

D_{BB} is budburst day and N_{LMAmax} the day when LMA reaches its maximum value. The LMA algorithm was conceived in a way to allow for the simulation of the LMA distribution inside the canopy and its seasonal dynamics. The choice of the algorithm was theoretically based on the observed LMA and PAR profiles in comparison to the LAI profiles. The PAR profile approximately follows the Lambert-Beer law (Monsi and Saeki, 1953) and the absorbed PAR (m^{-2} leaves) by a given LAI layer ($I_{\text{layer } i}$) is modelled by the following equation:

$$I_{\text{layer } i} = \alpha I_{\text{ref}} \exp(-k_{\text{PAR}} L) \frac{1 - \exp(-k_{\text{PAR}} \varepsilon)}{\varepsilon} \quad (3)$$

with L the leaf area index above the layer i , I_{ref} the measured PAR above the canopy, α the layer absorbance and ε the LAI layer thickness. If ε is small enough Eq. (3) becomes:

$$I_{\text{layer } i} = k_{\text{PAR}} \alpha \text{PAR}_{\text{ref}} \exp(-k_{\text{PAR}} L) \quad (4)$$

The same equation may be written as follows:

$$L = -\frac{1}{k_{\text{PAR}}} \ln \left(\frac{I_{\text{layer } i}}{k_{\text{PAR}} \alpha I_{\text{ref}}} \right) \quad (4a)$$

On the other hand, the LMA profile may also be expressed with an exponential relationship (Rambal et al., 1996).

$$\frac{\text{LMA}_{\text{layer } i}}{\text{LMA}_{\text{sunleaves}}} = \exp(-k_{\text{LMA}} L) \quad (5)$$

With $\text{LMA}_{\text{sunleaves}}$ the LMA of sun leaves. By combining Eqs. (4a) and (5), a relationship between LMA and PAR was deduced.

$$\text{LMA}_{\text{layer } i} = \text{LMA}_{\text{sunleaves}} \left(\frac{I_{\text{layer } i}}{k_{\text{PAR}} \alpha I_{\text{ref}}} \right)^{k_{\text{LMA}}/k_{\text{PAR}}} \quad (6)$$

Eq. (6) gives only the form of a possible relationship between LMA of a canopy layer i , and the absorbed PAR by the same layer. To simulate both LMA decrease within canopy and LMA dynamics with time (including the value of LMA at maturity of leaves), LMA of the layer i ($\text{LMA}_{\text{layer } i}$) was linked to the sum of PAR absorbed by the layer during the leaf growth period. Eq.

(6) is thus reformulated as follows:

$$\text{LMA}_{\text{layer } i} [\text{day } d] = \sigma_{\text{LMA}} \left(\sum I_{\text{layer } i} \right)^{\rho_{\text{LMA}}} \quad (7)$$

ρ_{LMA} (without unit) and σ_{LMA} ($\text{g}_{\text{DM}} \text{MJ}^{-1}$) are two parameters and $I_{\text{layer } i}$, the sum of the PAR absorbed by the LAI layer i , from the budburst to the day d . In this way, we show that a relationship reproducing the LMA profile based on absorbed PAR is not linear if k_{LMA} differs from k_{PAR} , i.e. $\rho_{\text{LMA}} = k_{\text{LMA}}/k_{\text{PAR}} \neq 1$; in other words when the LMA profile differs from the PAR profile, what implies an imperfect acclimation for canopy carbon balance. In this equation, for a given LAI, σ_{LMA} controls the total foliar biomass, while ρ_{LMA} drives more its distribution in the canopy depth. σ_{LMA} represents a factor of energy conversion from PAR to dry matter produced, while ρ_{LMA} quantifies the level of acclimation of the LMA profile to the light.

This equation is modified to take into account two biological phenomena. Firstly, when budburst occurs, leaves have a thickness and a LMA different from zero. To take into account for this phenomenon, a constant is added to the relationship, which is considered a species-specific parameter ($\text{LMA}_{\text{basic}}$). Secondly, the temporal dynamics is corrected using the ratio between temperature sum (S_{frCLMA}) and the critical value (F_{critLMA}) in order to reproduce the “growth curve” of LMA from budburst to leaves maturity. This ratio depending on degree-days goes from 0 at budburst to 1 when leaf maturity is achieved (i.e. when LMA has reached its maximum value). This ratio reproduces a smaller mass growth rate at the beginning of growth and takes also into account the temperature effect on LMA dynamics with time.

Finally the proposed LMA algorithm is:

$$\begin{aligned} \text{LMA}_{\text{layer } i} [\text{day } d] \\ = \text{LMA}_{\text{basic}} + \frac{S_{\text{frCLMA}}}{F_{\text{critLMA}}} \sigma_{\text{LMA}} \left(\sum_{\text{budburst}}^d I_{\text{layer } i} \right)^{\rho_{\text{LMA}}} \end{aligned} \quad (8)$$

Then, the LMA sub-model is coupled with the CASTANEA model. Instead of using a constant value of LMA for the sun leaves and a decreasing exponential relationship to assess the LMA profile (Dufrene et al., 2005), the LMA in each layer of canopy is calculated every day (according to Eq. (8)), using the sum of the absorbed PAR calculated by CASTANEA.

2.5. Parameterization and validation of the LMA sub-model

Four parameters were to be estimated: the critical value of the temperature sum (F_{critLMA}) and the three other parameters of the final Eq. (7): σ_{LMA} , ρ_{LMA} and $\text{LMA}_{\text{basic}}$.

Few data were available for LMA dynamics during leaf maturation phase on mature beech trees: measurements in the Italian site of Collelongo in 1995 (Matteucci, 1998), a study from Schulte (1993) in the German site of Solling (1986–1988), an unpublished experiment on mature trees during 1998 in Orsay (France) and a monitoring in Hesse in 1998 (Montpied, personal communication). The critical value of state of forcing (from budburst to leaf maturity) is determined by averaging results from all experiments ($424^\circ \text{C day} \pm 81$).

Table 2 – Extinction coefficients of light (k_{PAR}) calculated using the simulated and measured profiles of PAR in the canopy in Hesse (1997)

Julian day (1997)	Solar elevation (GMT)	r^2	N	Measured k_{PAR}	Simulated k_{PAR}
217	14h56	0.74	45	0.63	0.66
223	8h41	0.55	73	0.69	0.72
223	10h07	0.43	73	0.65	0.61
223	11h46	0.66	73	0.64	0.61
232	12h47	0.80	75	0.67	0.66
232	14h45	0.68	78	0.59	0.66
	Mean			0.65	0.65

Measurements were made for different days and solar elevations. The correlation coefficient (r^2) of the relationship between the measurements and the fitted exponential function and the sample size (N) are given.

The ρ_{LMA} is estimated in 1997 in Hesse, knowing both the measured k_{LMA} and k_{PAR} . The LMA_{basic} is fixed respectively to 10, 20 and 130 $g_{DM} m^{-2}$ for beech, sessile oak and holm oak to reproduce the variability between the species based on literature and our measurements (Davi, 2004). Finally, the σ_{LMA} , was deduced from Eq. (8) for the sun leaves at maturity in Hesse in 1997, knowing ρ_{LMA} , LMA_{basic} and the sum of the absorbed PAR during the period.

For LMA simulation at maturity, the LMA sub-model (σ_{LMA} , ρ_{LMA} , LMA_{basic}) is only calibrated, using profiles from Hesse in 1997. Data from Hesse in 1998, and 1999, Fougères in 1998 and 1999 and Solling from 1986 to 1988 were independent of data from Hesse 1997 and allow an independent validation. The profiles in Puéchabon and Champenoux allow for an evaluation of the algorithms generality. Two kinds of results are presented in this paper:

- The profiles of simulated and measured LMA in Hesse in 1997, where the LMA sub-model is parameterized, in Hesse (1998, 1999) and Fougères (1998, 1999), where a validation of the LMA sub-model is assessed, Puéchabon (1999) and Champenoux (1999), where the generality of the LMA sub-model is estimated.
- The temporal dynamics of LMA through the year in Hesse (1998) and Solling (1986). Only the form of the dynamics is validated. The date of leaf maturity (i.e. when LMA reaches to its maximum value), is not validated since it is calculated using $F_{critLMA}$ calculated with these data plus others.

2.6. Sensitivity analysis

Using the data parameterization described above, a sensitivity analysis is done by changing simultaneously both ρ_{LMA} and σ_{LMA} values. In this analysis, ρ_{LMA} varied from 0.1 to 1 with a step of 0.05 and σ_{LMA} from 2 to 40 using a step of 2. These bounds were chosen to allow the simulation of a sufficiently large range of LMA. The sensitivity analysis was done for the Hesse site from 1997 to 2003: a period of 7 years representing a large range of weather variability, including a hot summer with a strong drought in 2003. Two simulated outputs of the coupled model (LMA sub-model and CASTANEA model) were investigated: the LMA of the sun leaves and the canopy carbon net gain (C_{net}) defined as the difference between the gross primary production (GPP) and the canopy cost: sum of biomass growth (GB_{leaves}), growth respiration (RG_{leaves}) and maintenance respiration (RM_{leaves}) of leaves.

$$C_{net} = GPP - GB_{leaves} - RM_{leaves} - RG_{leaves} \tag{9}$$

3. Results

3.1. Synthesis of measurements

The relationship between the PAR and the LAI was a negative exponential, whose extinction coefficient (k_{PAR}) was 0.65 on

Table 3 – Review of the leaf area index (LAI), leaf mass per area (LMA) measurements in $g_{DM} m^{-2}$ for sun and shade leaves, and the corresponding exponential decrease coefficient (k_{LMA})

Site	Species	Year	LAI ($m^2 m^{-2}$)	$LMA_{sunleaves}$ ($g_{DM} m^{-2}$)	$LMA_{shadeleaves}$ ($g_{DM} m^{-2}$)	Fitted k_{LMA}
Hesse	<i>Fagus sylvatica</i>	1997	5.3	95	38	0.19
Hesse	<i>Fagus sylvatica</i>	1998	7.0	102	25	0.17
Hesse	<i>Fagus sylvatica</i>	1999	5.9	115	29	0.18
Fougères	<i>Fagus sylvatica</i>	1998	8.2	101	25	0.19
Fougères	<i>Fagus sylvatica</i>	1999	7.8	100	25	0.19
Solling	<i>Fagus sylvatica</i>	1986	5.1	105	47 ^a	
Solling	<i>Fagus sylvatica</i>	1987	6.2	103	58 ^a	
Solling	<i>Fagus sylvatica</i>	1988	5.4	98	51 ^a	
Champenoux	<i>Quercus petraea</i>	1999	3.9	106	55	0.18
Puéchabon	<i>Quercus ilex</i>	1999	2.3	244	172	0.14

^a From Schulte (1993); probably an average value higher than for the lower leaves in the canopy.

average (Table 2). Although the relationship was always significant, the amount of explained variance was relatively variable (ranged between 43 and 80%).

The measured LMA for sun ($LMA_{sunleaves}$) and shade ($LMA_{shadeleaves}$) leaves and the rate of the negative exponential relationship fitted on the measured LMA profile (k_{LMA}) are summarized for all sites and years in Table 3. The $LMA_{sunleaves}$ of beech and deciduous oak varied little from 95 to $106 \text{ g}_{DM} \text{ m}^{-2}$ between sites and years, except in Hesse in 1999 ($115 \text{ g}_{DM} \text{ m}^{-2}$). The $LMA_{shadeleaves}$ showed more variability. If only data measured on an entire profile were kept, this variability was explained by the measured LAI ($r^2 = 0.84$). The higher the LAI, the lower was $LMA_{shadeleaves}$, because shade leaves receive less light. The LMA of the holm oak, which is an evergreen species, was much higher than the LMA of the deciduous species.

In Hesse, the measured nitrogen content per biomass unit (i.e. concentration $g_N \text{ g}_{DM}^{-1}$) showed little variation within the canopy (Fig. 1). For the three years of study in Hesse, the nitrogen content was slightly lower in the upper part of the canopy. As opposed to this, in Puéchabon (holm oak) the nitrogen content per unit mass was independent of the canopy depth (data not shown). In Hesse, the whole nitrogen content in the canopy, per soil surface unit, varied from 8.25, 8.92 and 9.46 g_N in $\text{leaves m}_{soil}^{-2}$, respectively for 1997, 1998 and 1999.

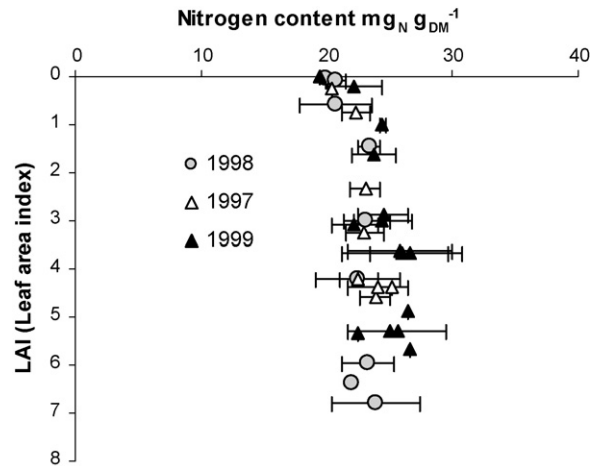


Fig. 1 – Measured leaf nitrogen content (in $\text{mg}_N \text{ g}_{DM}^{-1}$) in function of the canopy depth expressed in leaf area index (LAI), in Hesse in 1997, 1998 and 1999 for beech.

3.2. Model calibration and validation

The model calibration was done with data from the Hesse site in 1997. The coefficients of the exponential decrease within the canopy were 0.65 for PAR extinction and 0.19 for LMA

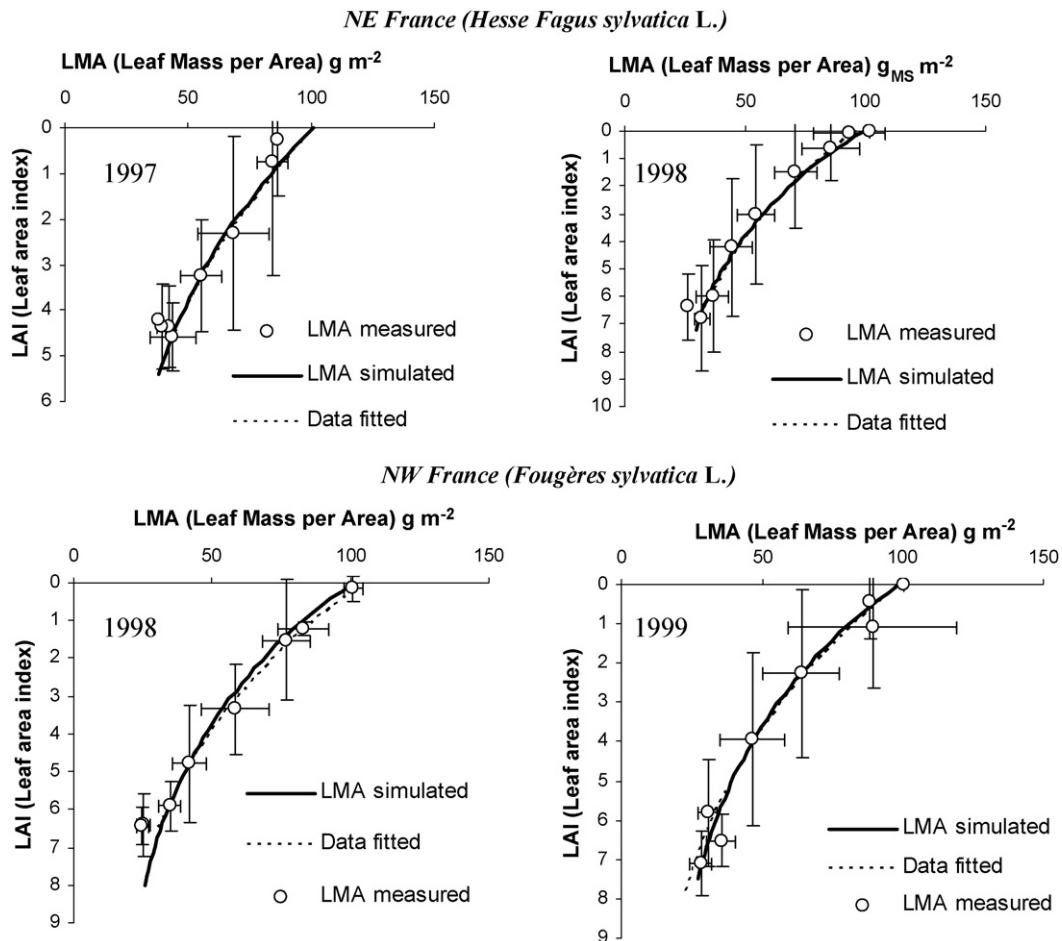


Fig. 2 – Measured and simulated leaf mass per area (in $\text{g}_{DM} \text{ m}_{leaves}^{-2}$) in function of the canopy depth expressed in leaf area index (LAI), in Hesse in 1997, 1998 and Fougères in 1998 and 1999 for beech. Error bar are indicated.

Table 4 – Summary of the parameterization of the LMA sub-model			
Symbol	Unit	Value	Species
$F_{critLMA}$	°C	424	All
ρ_{LMA}	–	0.29	All
σ_{LMA}	$g_{DM} MJ^{-1}$	21	All
LMA_{basic}	$g_{DM} m_{leaves}^{-2}$	10	<i>Fagus sylvatica</i>
LMA_{basic}	$g_{DM} m_{leaves}^{-2}$	20	<i>Quercus petraea</i>
LMA_{basic}	$g_{DM} m_{leaves}^{-2}$	130	<i>Quercus ilex</i>

decrease (Table 3). From these estimates, a value for ρ_{LMA} of 0.29 (0.19/0.65) was deduced. The σ_{LMA} value was then calculated by inverting Eq. (7) for the sun leaves at maturity in Hesse in 1997. The simulated growth length was 34 days in 1997 and at the end of the growth period the sum of the PAR absorbed by the sun leaves was $163 MJ m_{leaves}^{-2}$. This resulted in a σ_{LMA} value of 21. The complete parameterization of the LMA sub-model is summarized in Table 4.

Fig. 2 shows the results of this parameterization on the simulated LMA profiles in Hesse in 1997 and 1998 and in Fougères in 1998 and 1999. In all cases, the simulated LMA was very close both to the measurements and to the fitted exponential relationship. The LMA sub-model was also able to accurately reproduce the LMA profiles for the sessile oak and the holm oak (Fig. 3). However, the model was not able to reproduce one LMA profile at our disposal (Fig. 4). For Hesse in 1999, following a thinning during the winter 1998–1999, the model did not reproduce the high LMA value, measured on the leaves located in the upper part (2/3) of the canopy. The simulated LMA values of sun and shade leaves reported in Table 3 fitted well the measurements (Fig. 5), and the LMA sub-model accurately simulated the variability in LMA canopy profiles across species and sites.

The ability of the model to describe the LMA dynamics during the season was also tested (Fig. 6). Both in Hesse (in 1998) and in Solling (in 1986), the LMA sub-model properly simulated the LMA evolution. In Hesse during 1998, the leaf growth period lasted 30 days and the peak of the simulated

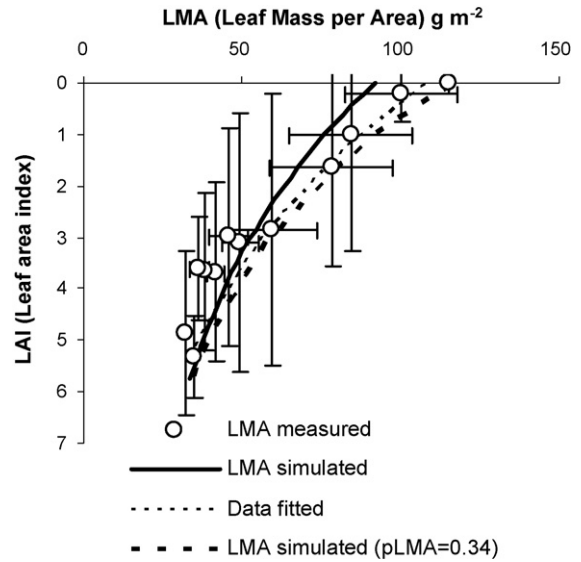


Fig. 4 – Measured and simulated leaf mass per area (in $g_{DM} m_{leaves}^{-2}$) in function of the canopy depth expressed in leaf area index (LAI), in Hesse in 1999 following a forest cut in winter.

LMA growth rate was met at the 17th day after the budburst. Subsequently the rate diminished until the end of the leaf growth period.

3.3. Sensitivity analysis

The results of the sensitivity analysis for the two parameters (σ_{LMA} and ρ_{LMA}) are presented in graphics that correspond to a projection of 3D graphics on a plane (Fig. 7). The parameterized ρ_{LMA} and σ_{LMA} in Hesse 1997 constituted a couple of values (ρ_{LMA}, σ_{LMA}) = (0.29, 21) that is indicated by a white cross in the four graphics. When ρ_{LMA} and σ_{LMA} increase (Fig. 7a), $LMA_{sunleaves}$ increases from LMA_{basic} to up to $300 g_{DM} m^{-2}$. The yearly canopy carbon net gain (i.e. canopy production minus

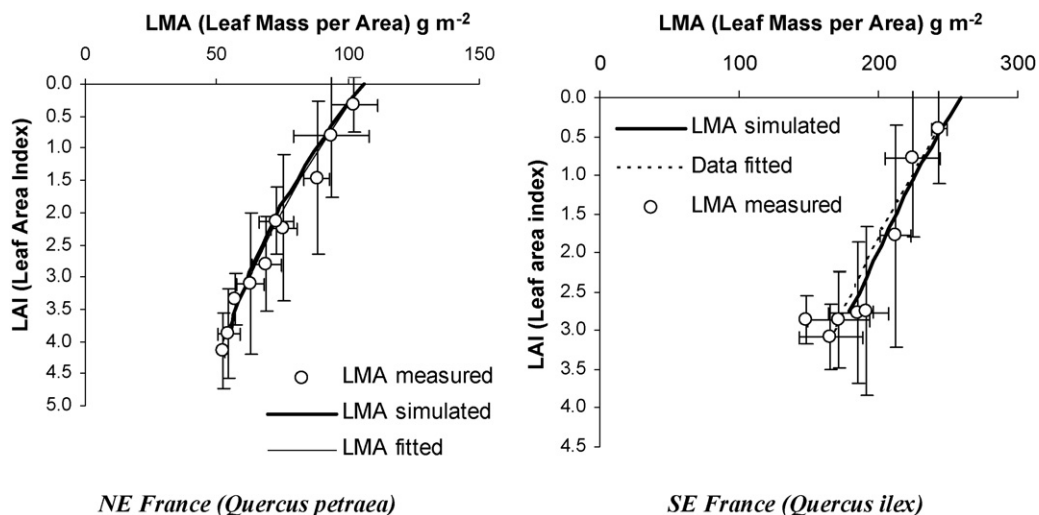


Fig. 3 – Measured and simulated leaf mass per area (in $g_{DM} m_{leaves}^{-2}$) depending on the canopy depth expressed in leaf area index (LAI), in Puéchabon and Champenoux in 1999 respectively for holm and sessile oaks. Error bar are indicated.

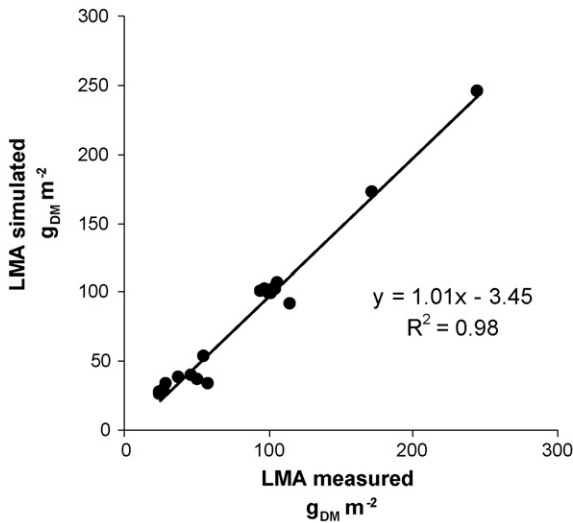


Fig. 5 – Measured versus simulated leaf mass per area (in $g_{DM} m^{-2}_{leaves}$) of sun and shade leaves for all sites and years reported in Table 3.

canopy cost) was maximised for an area of $(\rho_{LMA}, \sigma_{LMA})$ couples ranging between (0.4, 15) and (0.9, 4). The couple measured in Hesse in 1997 was not included in this area and was not optimal in terms of carbon gain (Fig. 7b).

4. Discussion

Several authors have already proposed to use incident or absorbed PAR to drive the leaf mass growth (Niinemets, 1995). However, linear relationships were often used (Niinemets, 1995; Niinemets et al., 2004) and the same algorithm could not predict vertical LMA distribution, seasonal dynamics and average values for various sites, year and species at the same time. For all empirical canopy profiles presented here, PAR decreased more steeply than LMA. Consequently,

a linear relationship between absorbed PAR and LMA cannot reproduce the observed LMA profiles. Rosati et al. (2001) arrived at the same conclusion; they found a good relationship between the square root of daily interception of light and LMA in aubergine (*Solanum melongena* L.). Meir et al. (2002) investigated the relationships between maximum carboxylation capacity (V_{cmax}) and the incident irradiance (Q) for several forest species. They found a linear relationship between $\ln(V_{cmax})$ and $\ln(Q)$. In CASTANEA, V_{cmax} is linearly related to the nitrogen per unit surface area and to the LMA (Eq. (1), with nitrogen concentration being constant per mass unit within the canopy). Consequently, our algorithm to simulate the LMA (Eq. (8)) is consistent with the results of Meir et al. (2002).

A strict linear relationship between absorbed PAR and LMA did not lead to model outputs that describe all the variability of LMA between stands receiving the same amount of light. And yet, in neighbouring beech stands, LMA of the sun leaves showed a spatial variation of more and less 10% between trees for a same year (Bouriaud, 2003; Davi et al., 2006). These variations were probably correlated to the soil fertility or the tree age. Using a LMA_{basic} that varies according to the site, the year or the species, allows to easily take into account these multiple sources of variability. The irradiance of the previous year can affect LMA of the current year (Eschrich et al., 1989; Uemura et al., 2000) through complex ways. For beech, the number of cells in palisade parenchyma was determined in the buds at the middle of the summer of the previous year. This phenomenon can partly elucidate why in Hesse with the same parameterization used in 1998 and 1997, the measured profile could not be explained in 1999 by the LMA-sub-model. Between the summer 1998 and spring 1999, some shade buds were exposed to the sun following the thinning. Consequently, the model overestimated the LMA at the middle of the crown (Fig. 4), because it does not take into account that these leaves were formed as shade leaves in the buds (with few layers of cells). In addition, the model strongly underestimated the LMA for the sun leaves likely because the carbon, not used for the shade leaves, was probably re-allocated to the sun leaves. To conclude, the sensi-

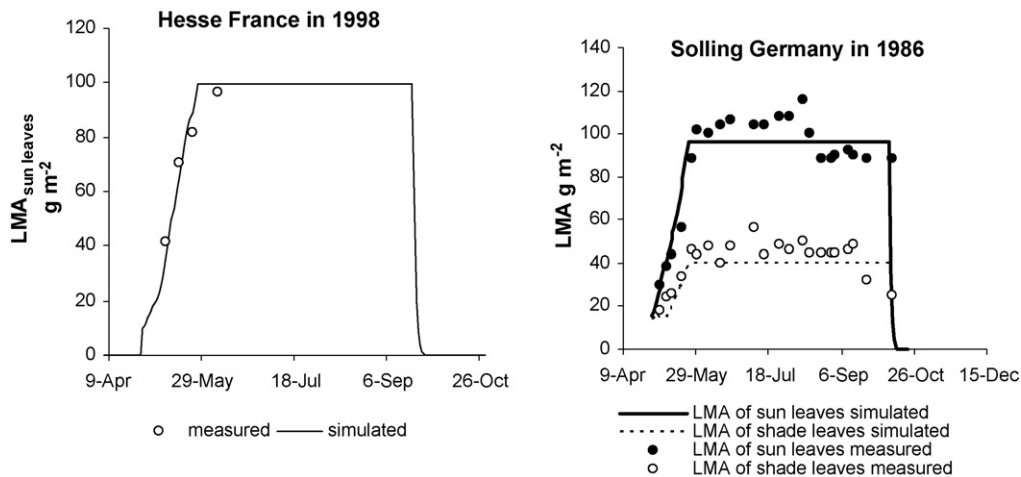


Fig. 6 – Measured and simulated leaf mass per area (in $g_{DM} m^{-2}_{leaves}$) in function of time in Hesse in 1999 and in Solling in 1986 (the last redrawn from Schulte, 1993).

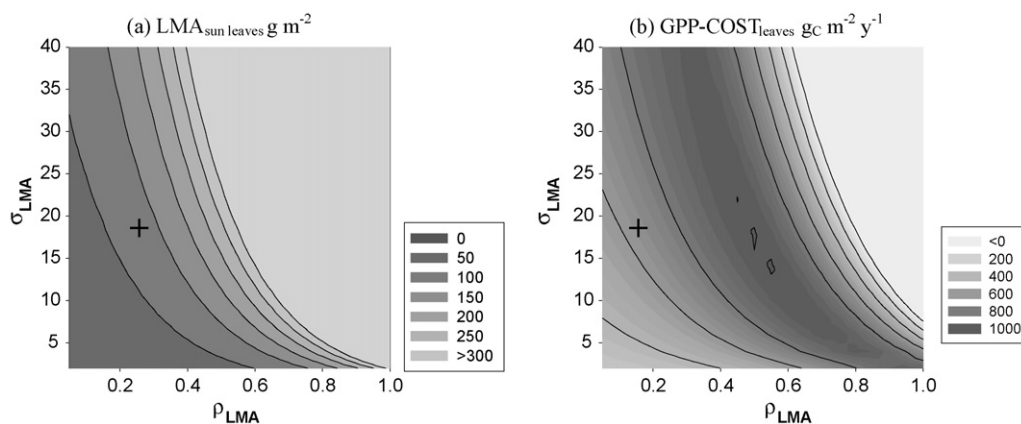


Fig. 7 – Sensitive analysis of the simulated (a) leaf mass per area of sun leaves ($LMA_{\text{sun leaves}}$), and (b) canopy carbon net gain (canopy production minus canopy cost), to the ρ_{LMA} (g DM MJ^{-1}) and σ_{LMA} (without unit) parameters in Hesse from 1997 to 2003.

tive analysis indicate that as already found in previous studies (Evans and Poorter, 2001), the LMA distribution measured on forest canopies was shown to be not fully optimized for the carbon gain.

Acknowledgements

We would like to thank all the people, who facilitated us the access to the data: especially the team that manages the Fougères sites (particularly Claude Nys).

REFERENCES

- Andersson, B., Aro, E.M., 1997. Proteolytic activities and proteases of plant chloroplasts. *Physiol. Plant.* 100, 780–793.
- Ball, J.T., Woodrow, I.E., Berry, J.A., 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggins, J. (Ed.), *Progress in Photosynthesis Research*, vol. 4, pp. 221–224.
- Bertin, N., Gary, C., 1998. Short and long term fluctuations of the leaf mass per area of tomato: implications for growth models. *Ann. Bot.* 82, 71–81.
- Bréda, H., Granier, A., Aussenac, G., 1995. Effects on thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt) Liebl.). *Tree Physiol.* 15, 295–306.
- Björkman, O., 1981. Responses to different quantum flux densities. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), *Physiological Plant Ecology. I: Responses to the Physical Environment*. Encyclopedia of Plant Physiology, New Series, vol. 12A. Springer-Verlag, Berlin, pp. 57–107.
- Bouriaud, O., 2003. Analyse fonctionnelle de la productivité du hêtre: influences des conditions de milieu, de la structure du peuplement et du couvert, effets de l'éclaircie. Thèse de Doct. en Sciences forestière, ENGREF, 240 p+annexes.
- Bossel, H., 1996. TREEDYN3 forest simulation model. *Ecol. Modell.* 90 (3–1), 187–227.
- Castro-Díez, P., Puyravaud, J.P., Cornelissen, J.H.C., 2000. Leaf structure and anatomy as related to leaf mass per area variation in seedlings of a wide range of woody plant species and types. *Oecologia* 124, 476–486.
- Chabot, B.F., Hicks, D.J., 1982. The ecology of leaf life spans. *Annu. Rev. Ecol. Syst.* 13, 229–259.
- Chapin, F.S., 1991. Integrated responses of plant to stress. *Bioscience* 41, 28–36.
- Davi, H., 2004. Développement d'un modèle générique simulant les flux et les stocks de carbone et d'eau dans le cadre des changements climatiques. Thèse de Doct. en Sci., Univ. Paris-Sud, Orsay, 213 p+annexes.
- Davi, H., Dufrêne, E., Granier, A., Le Dantec, V., Barbaroux, B., François, C., Bréda, N., Montpied, P., 2005. Modelling carbon and water cycles in a beech forest. Part II: Validation for each individual processes from organ to stand scale. *Ecol. Modell.* 185 (2–4), 387–405.
- Davi, H., Bouriaud, O., Dufrêne, E., Soudani, S., Pontaillier, J.Y., le Maire, G., François, C., Bréda, N., Granier, A., le Dantec, V., 2006. Effect of spatial parameters aggregation for modelling carbon and water fluxes in forest ecosystems. *Agric. For. Meteorol.* 139, 269–287.
- Dufrêne, E., Davi, H., François, C., le Maire, G., Le Dantec, V., Granier, A., 2005. Modelling carbon and water cycles in a Beech forest. Part I: Model description and uncertainty analysis on modelled NEE. *Ecol. Modell.* 185 (2–4), 407–436.
- Dufrêne, E., Bréda, N., 1995. Estimation of deciduous forest leaf area index using direct and indirect methods. *Oecologia* 104, 156–162.
- Eschrich, W., Burchardt, R., Essiamah, S., 1989. The induction of sun and shade leaves of the European beech (*Fagus sylvatica* L.): anatomical studies. *Trees* 3, 1–10.
- Evans, J.R., Poorter, H., 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximising carbon gain. *Plant Cell Environ.* 24, 755–767.
- Farquhar, G.D., von Caemmerer, S., Berry, J.A., 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. *Planta* 149, 78–80.
- Field, C.B., 1983. Allocating leaf nitrogen for maximization of carbon gain leaf age as a control on the allocation program. *Oecologia* 56, 348–355.
- Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3 0). *Ecol. Modell.* 95 (2–3), 249–287.

- Garnier, E., 1992. Growth analysis of congeneric annual and perennial grass species. *J. Ecol.* 80, 665–675.
- Gracia, C.A., Tello, E., Sabate, S., Bellot, J., 1999. GOTLWA: An integrated model of water dynamics and forest growth. In: Roda, F., Retana, J., Garcia, C.A., Bellot, J. (Eds.), *Impacts of Global Change on Tree Physiology and Forest Ecosystems*. Springer-Verlag, Berlin.
- Granier, A., Ceschia, E., Damesin, C., Dufrêne, E., Epron, D., Gross, P., Lebaube, S., Le Dantec, V., Le Goff, N., Lemoine, D., Lucot, E., Ottorini, J.M., Pontailler, J.Y., Saugier, B., 2000. The carbon balance of a young beech forest. *Funct. Ecol.* 14, 312–325.
- Green, D.S., Erickson, J.E., Kruger, E.L., 2003. Foliar morphology and canopy nitrogen as predictors light-use efficiency in terrestrial vegetation. *Agric. For. Meteorol.* 115, 163–171.
- Groot, C.J., Lantinga, E.A., 2004. An object-oriented model of the morphological development and digestibility of perennial ryegrass. *Ecol. Modell.* 177 (3–4, 1), 297–312.
- Hanson, H.C., 1917. Leaf-structure as related to environment. *Am. J. Bot.* 4, 533–560.
- Hoff, C., Rambal, S., Joffre, R., 2002. Simulating carbon and water flows and growth in a Mediterranean evergreen *Quercus ilex* coppice using the FOREST-BGC model. *For. Ecol. Manage.* 164, 121–136.
- Hollinger, D., 1996. Optimality and nitrogen allocation in a tree canopy. *Tree Physiol.* 133, 216–221.
- Idso, S.B., 1981. A set of equations for full spectrum and 8 to 14 μm and 10.5 to 12.5 μm thermal radiation from cloudless skies. *Water Resour. Res.* 17 (2), 295–304.
- Jayasekera, R., Schleser, G.H., 1988. Seasonal changes in potential net photosynthesis of sun and shade leaves of *Fagus sylvatica* L. *J. Plant Physiol.* 133, 216–221.
- Kätterer, T., Eckersten, H., Andrén, O., Pettersson, R., 1997. Winter wheat biomass and nitrogen dynamics under different fertilization and water regimes: application of a crop growth model. *Ecol. Modell.* 102 (2–3), 301–314.
- King, D.A., 2005. Linking tree form, allocation and growth with an allometrically explicit model. *Ecol. Modell.* 185, 77–91.
- Kull, O., 2002. Acclimation of photosynthesis in canopies: models and limitations. *Oecologia* 133, 267–279.
- Lambers, H., Poorter, H., 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23, 187–261.
- Lebre, M., Nys, C., Forgeard, F., 2001. Litter production in an Atlantic beech (*Fagus sylvatica* L.) time sequence. *Ann. For. Sci.* 58, 755–768.
- Leuning, R., 1997. Scaling to common temperature improves the correlation between the photosynthesis parameters J_{max} and V_{cmax} . *J. Exp. Bot.* 48, 345–347.
- Matteucci, G., 1998. Bilancio del carbonio in una faggetta dell'Italia Centro-Meridionale: determinanti ecofisiologici, integrazione a livello di copertura e simulazione dell'impatto dei cambiamenti ambientali Tesi di dottorato. Università degli studi di Padova, Padova, 227 pp.
- Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O.F., Carswell, F., Nobre, A., Jarvis, P.G., 2002. Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. *Plant Cell Environ.* 25, 343–357.
- Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jpn. J. Bot.* 14, 22–52.
- Niinemets, U., Kull, O., Tenhunen, J.D., 2004. Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. *Plant Cell Environ.* 27, 293–313.
- Niinemets, U., 1999. Energy requirement for foliage formation is not constant along canopy light gradients in temperate deciduous trees. *New Phytol.* 141, 459–470.
- Niinemets, U., 1995. Distribution of foliar carbon and nitrogen across the canopy of *Fagus sylvatica*: adaptation to a vertical light gradient. *Acta Oecol.* 16 (5), 525–541.
- Niinemets, U., Kull, O., 1995. Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphology plasticity. *Tree Physiol.* 18, 681–696.
- Olthof, I., King, D.J., 2000. Development of a forest health index using multispectral airborne digital camera imagery. *Can. J. Remote Sens.* 3 (26), 166–176.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matters levels in great plains grasslands. *Soil Sci. Soc. Am. J.* 51, 1173–1179.
- Pons, T.L., Jordi, W., Kuiper, D., 2001. Acclimation of plants to light gradients in leaf canopies: evidence for a possible role of cytokinins transported in the transpiration stream. *J. Exp. Bot.* 52 (360), 1563–1574.
- Poorter, H., Evans, J.R., 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia* 116, 26–37.
- Rambal, S., Damesin, C., Joffre, R., Methy, M., Lo Seen, D., 1996. Optimization of carbon gain in canopies of Mediterranean evergreen oaks. *Ann. For. Sci.* 53, 547–560.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: a global convergence in plant functioning. *Proc. Natl. Acad. Sci. U.S.A.* 94, 13730–13734.
- Rosati, A., Badeck, F.W., Dejong, M., 2001. Estimating light canopy interception and absorption using leaf mass per unit leaf area in *Solanum melongena*. *Ann. Bot.* 88, 101–109.
- Rousseau, M.C., Hall, A.J., Sanchez, R.A., 1996. Far-red enrichment and photosynthetically active radiation level influence leaf senescence in field-grown sunflower. *Physiol. Plant.* 86, 398–406.
- Running, S.W., Coughlan, J.C., 1998. A general model of forest ecosystem processes for regional applications. I: Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Modell.* 42, 125–154.
- Ryan, G.M., 1991. Effects of climate change on plant respiration. *Ecol. Appl.* 1 (2), 157–167.
- Schulte, M., 1993. Saisonale und interannuelle Variabilität des CO_2 -Gaswechsels von Buchen (*Fagus sylvatica* L.). In: Bestimmung von C-Bilanzen mit Hilfe eines empirischen Modells. Verlag Shaker, Aachen.
- Simeoni, G., Le Roux, X., Gignoux, J., Sinoquet, H., 2000. Treegrass: a 3D, process-based model for simulating plant interactions in tree-grass ecosystems. *Ecol. Modell.* 131 (1, 30), 47–63.
- Spitters, C.J.T., 1986. Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. Part II: Calculation of canopy photosynthesis. *Agric. For. Meteorol.* 38, 231–242.
- Uemura, A., Ishida, A., Takashi, N., Ichiro, T., Tanabe, H., Matsumoto, Y., 2000. Acclimation of leaf characteristics of *Fagus* species to previous year and current year solar irradiances. *Tree Physiol.* 20, 945–951.
- Van Volkenburgh, E., 1999. Leaf-expansion an integrating plant behaviour. *Plant Cell Environ.* 22, 1463–1473.
- Verhoef, W., 1984. Light scattering by leaf layers with application to canopy reflectance modeling: the SAIL model. *Remote Sens. Environ.* 16, 125–141.
- Verhoef, W., 1985. Earth observation modelling based on layer scattering matrices. *Remote Sens. Environ.* 17, 165–178.
- Vose, J.M., Bolstad, B.V., 1999. Challenges to modelling NPP in diverse eastern deciduous forests: species-level comparisons of foliar respiration responses to temperature and nitrogen. *Ecol. Modell.* 122 (3), 165–174.

- Warren, C.R., Adams, M.A., 2001. Distribution of N, Rubisco and photosynthesis in *Pinus pinaster* and acclimation to light. *Plant Cell Environ.* 24, 597–609.
- Welles, J.M., Norman, J.M., 1991. Instrument for indirect measurement of canopy architecture. *Agron. J.* 83, 818–825.
- Wirtz, K.W., 2000. Simulating the dynamics of leaf physiology and morphology with an extended optimality approach. *Ann. Bot.* 86 (4), 753–764.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., et al., 2005. Assessing the generality of global leaf trait relationships. *New Phytol.* 166 (2), 485–496.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., et al., 2004. The worldwide leaf economics spectrum. *Nature* 428 (6985), 821–827.