PART OF A SPECIAL ISSUE ON FUNCTIONAL–STRUCTURAL PLANT MODELLING

Assessing the effects of management on forest growth across France: insights from a new functional–structural model

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Received: 29 October 2013 Returned for revision: 21 January 2014 Accepted: 27 February 2014 Published electronically: 25 April 2014

INTRODUCTION

The current increase in drought intensity and frequency (IPCC, 2014) has been recognized as a probable cause of forest die-back (e.g. Anderegg et al., 2012) and is expected to affect forests greatly worldwide (Allen et al., 2010; Lindner et al., 2010). The assessment and projection of climate change effects on forests often use growth as a surrogate for tree vitality (Bigler and Bugmann, 2003; Dobbertin, 2005). Indeed, growth has long been considered as an integrated signal of biotic and abiotic factors that reflect the functioning of the whole tree (Cook, 1985). Long-term low growth is a well-known trait of dying trees, and growth has been reported to be an important variable for tree mortality (Bigler and Bugmann, 2003) or species range (Benito-Garzón et al., 2013) projections. Long-term projections of forest stand growth under a rapidly changing environment is consequently an important modelling goal (Lara et al., 2013).

So far, projections of effects of climate change on forest growth have principally relied on ecophysiological process-based models (PBMs) validated at the stand rotation time scale (Pretzsch et al., 2008; Fontes et al., 2010). PBMs provide a framework to formalize biophysical hypotheses and combine knowledge about the physiological mechanisms that determine forest functioning and growth. PBMs can be evaluated at different temporal and spatial scales according to the process of interest (leaf or canopy matter and energy fluxes, stand or tree growth, or distributional range) and can therefore be used to investigate how tree functions will change in a changing environment (Mäkelä et al., 2000). Forest PBMs differ in their complexity, and one can separate ‘stand PBMs’ that aimed to predict growth, or carbon (C) and water fluxes at the stand scale, from tree-centred PBMs that aimed to simulate the functioning of each individual tree within a forest stand (Fontes et al., 2010). A recent study, however, has demonstrated that more robust results are obtained at the stand scale when stand
PBM s are used rather than aggregated predictions from tree-centred models (Cao, 2006). Moreover, tree-centred PBMs can hardly be used to simulate the long-term functioning of forests grown under contrasted conditions as they need a huge amount of data to be properly calibrated, and considerable computing power. As a consequence, few PBMs are able efficiently to simulate temporal changes in stand structure, i.e. changes in the distribution of the tree size features. In particular, most of them fail to predict the circumference and volume increments of the individual trees, as well as the evolution of tree density during the forest rotation.

However, the structure of forest stands has strong effects on the functioning of individual trees, through size and competition (Gomez-Aparicio et al., 2011). Competition intensity has been shown to modulate the stand growth responses to annual climate (Piutti and Cescatti, 1997; Magruder et al., 2013), and tree growth responses to environmental factors may be strongly affected by individual size (DeLuise et al., 2009; Mérian and Lebourgeois, 2011). Competition is also a major process involved in climate-driven forest die-back and mortality (Linares et al., 2010; Ruiz-Benito et al., 2013). These results suggest that silviculture, which controls the amount and distribution of available growing space in a stand, is of major importance for the mitigation of climate change effects on forests (Keenan, 2012; Vayreda et al., 2012). The inability of most stand PBMs to simulate stand structure consequently strongly limits their explorative capacity and their potential applications. First, they are not suitable for simulating the influence of forest management on forest functioning, precluding (1) the assessment of biomass stocks and sink capacities of the increasingly managed part of the world’s forests (Bellassen et al., 2011) and (2) the design of adaptive silvicultural guidelines taking into account current and future impacts of climate change. Secondly, stand PBMs without stand structure representation cannot be directly evaluated (i.e. without strong upscaling hypotheses) with the most abundant available data in forest science, namely dendrometric measurements from forest inventories (tree density or basal area) and dendrochronological series. The simulation of the stand structure would therefore allow modellers to formalize and to test functional hypotheses on the determination of growth at larger time and spatial scales, e.g. along contrasted regional or continental gradients. Finally, stand PBMs usually cannot accurately simulate processes intimately related to competition and stand structure, such as tree mortality (Bigler and Bugmann, 2003; McDowell et al., 2011) or productivity decline of aged stands (Binkley et al., 2002; Caspersen et al., 2011).

As a consequence, few recent attempts have been made to simulate the dynamics of forest structure within PBMs. Grote et al. (2011) complemented the MoBiLE-PSIM model with routines for average dimensional tree growth to improve the simulated C balance. Wang et al. (2011) simulated the impact of thinning on a coniferous forest within the TRIPLEX model using empirical prediction of the tree size distribution characteristics. In another approach, PBMs were coupled with empirical tree growth models to simulate the size trajectories of all the trees of a forest stand (Bellassen et al., 2010; Mäkelä et al., 2013; Poschenrieder et al., 2013). In a national-scale study, Bellassen et al. (2010) incorporated the fundamental rules of tree growth competition exposed in Dhôte (1999) into the global-scale PBM ORCHIDEE (Krinner et al., 2005). This work has been developed over a broad plant functional type. For this reason, it has two clear limits in that (1) it shows moderate agreement with observed data of forest productivity (Babst et al., 2013) and (2) it precludes accessing information on contrasted species-specific changes in stand structure (Knowles and Grant, 1983).

In contrast to the PBM approach, empirical tree-centred growth models proved their ability to predict temporal changes in forest structure on a purely statistical basis (Burkhardt and Tomé, 2012). The way resources are distributed among the individual trees, which is related to the tree growth performances (Nord-Larsen et al., 2006; Weiner and Damgaard, 2006), is the focal point of these models. Distribution of resources depends on the mode of tree competition (Weiner, 1990), which can be either size symmetric (i.e. growth is proportional to the size) when below-ground resources are limiting or size asymmetric when growth is predominantly limited by light (Schwinning and Weiner, 1998). Recent studies reported that the mode of competition can vary spatially, along ecological gradients (Pretzsch and Biber, 2010), but also temporally (Metsaranta and Lieffers, 2010; Zang et al., 2011). This fluctuation of the growth size asymmetry could thus be an important driver of the stand structure (Hara, 1988; Metsaranta and Lieffers, 2008) which is poorly considered in empirical tree-centred growth models. Previous studies conducted at both spatial and temporal scales reported a strong positive correlation between growth size asymmetry and productivity that can benefit tree-to-tree competition modelling (Pretzsch and Biber, 2010). Importantly, these empirical models cannot be used to project future impacts of climate change on a forest because they only seek to describe the statistical relationship among data, with no insight into the underlying, generalizable processes (Korzukhin et al., 1996).

In this study, our goal was to simulate the long-term temporal changes in stand structure of deciduous forests within a process-based model. We present CASTANEA–SSM, a new functional–structural plant model based on the coupling of the species-specific stand PBM CASTANEA with an empirical tree-centred module of growth competition (this stand structure module is hereafter referred to as SSM). Our modelling approach aimed to predict the size trajectories of every tree of a given stand during the forest rotation. Forest management has been considered by integrating a thinning-induced mortality algorithm at the tree level. The transient effect of thinning on canopy development, which can strongly affect tree water relations (Bréda et al., 1995; Rodríguez-Calçerrada et al., 2011), was assessed thanks to a new module of annual maximum leaf area index temporal dynamic.

After calibrating the SSM through a thorough analysis of the spatial and temporal variability of the mode of competition, we evaluated the fully coupled CASTANEA–SSM model over France for common beech (Fagus sylvatica) and temperate oak species (Quercus petraea and Quercus robur). Finally, we used the evaluated model to assess the potential of management practices to affect forest functioning at the country scale, by comparing the effect of contrasted silvicultural practices on simulated stand–atmosphere C fluxes and growth.
MATERIALS AND METHODS

Model structure: the CASTANEA PBM

The ecophysiological multilayer PBM CASTANEA (Dufreˆne et al., 2005) was used to simulate the annual stand growth of the study sites. CASTANEA aims at simulating C and water fluxes and stocks of an even-aged monospecific forest stand at the rotation time scale. Briefly, the stand simulated by CASTANEA comprises four functional compartments: foliage, woody biomass (including stem, branches and coarse roots), fine roots and the pool of carbohydrate reserves. The canopy is considered homogeneous horizontally and vertically sub-divided into a given number of layers, each of them enclosing a constant amount of leaf area. One of the major strengths of the model (Keenan et al., 2012) is its ability to reproduce the interannual fluctuations of C fluxes over Europe (Delpierre et al., 2012). A complete description of CASTANEA is given in Dufreˆne et al. (2005), with subsequent modifications from Davi et al. (2009) and Delpierre et al. (2012).

In this study, we used an improved version of the C allocation module (C. François and A. Cheaib, ESE, France, unpubl. res.). The variation in annual maximum leaf area index (LAI_max) of a given year is not only simulated according to seasonal climate (previous version), but also as a function of a soil water stress index (SWS_index, see ‘CASTANEA: soil water stress index’ in the Supplementary Data) defined on the previous year. The LAI_max value decreases when the SWS_index of the previous year is high, and increases otherwise. A maximum bound value of LAI_max is determined by an envelope curve depending on stand age. Additionally, the LAI_max value is reduced in the case of low carbohydrate reserve to prevent complete depletion of carbohydrate reserves (see ‘CASTANEA: inter-annual variation of LAI_max’ in the Supplementary Data). Carbon allocation to wood growth is determined annually as a fraction of gross primary productivity using allocation coefficients. Allocation coefficients are related to stand age, as well as to the current and previous year water stress (see ‘CASTANEA: inter-annual variation of wood growth’ in the Supplementary Data). The module of C allocation to wood growth was preliminary calibrated on RENECOFOR tree ring series (over the 1970–1990 period) to simulate the averaged above-ground biomass increment across stands.

Model structure: the empirical stand structure module (SSM)

The structure of the SSM is strongly inspired by the empirical tree-centred yield model FAGACEES (LeMouguédec and Dhôte 2011). The SSM works at a yearly time scale. It simulates (1) the distribution of the stand volume increment in a distribution of individual trees and (2) the mortality of individual trees (Fig. 1) resulting either from self-thinning or from commercial thinning, in the case of a managed stand.

Individual tree growth simulation relies on the following function (Deleuze et al., 2004; Fig. 1):

$$BAI_i = \frac{\sigma_{\text{sim}}}{2} \times \left[ \text{CBH}_i - m\sigma_{\text{sim}} + \sqrt{(m\sigma_{\text{sim}} + \text{CBH}_i)^2 - (4\sigma_{\text{sim}} \times \text{CBH}_i)} \right]$$

(1)

where CBH_i is the circumference at breast height of a given tree i and BAI_i is its corresponding annual basal area increment. In this
relationship, only trees with a circumference at breast height (CBH) above the threshold \( \sigma_{\text{aim}} \) which can be interpreted as the minimum circumference for direct access to sunlight, have a significant growth. Overstorey trees then grow proportionally to their size, following a slope coefficient \( \gamma_{\text{aim}} \) (Fig. 1). m is a smoothing parameter.

Natural tree mortality occurs when the stem density of the stand \( (N) \) exceeds the maximum density \( (N_{\text{max}}) \) allowed by the stand quadratic mean diameter \( (D) \):

\[
N_{\text{max}} = \frac{\alpha}{D^2}
\]

where \( \alpha \) and \( \beta \) are species-specific parameters (Charru et al., 2012) and

\[
D = \sqrt{\frac{1}{4\pi} \frac{\sum_{i=1}^{N} \text{CBH}_i^2}{N}}
\]

Based on these relationships, the relative density index \( \text{RDI} \) (Reineke, 1933) is defined as the ratio of actual to maximum density:

\[
\text{RDI} = \frac{N}{N_{\text{max}}}
\]

The RDI values range within the \([0,1]\) interval. Self-thinning (i.e. the mortality of the smallest trees) occurs when \( \text{RDI} = 1 \).

In managed stands, RDI is strongly modulated by intermediate thinning (Supplementary Data Fig. S1). In SSM, silvicultural scenarios are characterized by two parameters: \( \text{RDI}_{\text{initial}} \), the target RDI when the age of the stand is 0, and \( \text{RDI}_{\text{final}} \), the target RDI at the end of the stand rotation. Throughout the rotation, RDI is kept close to the RDI target value (Supplementary Data Fig. S1), with

\[
\text{RDI}_{\text{target}} = \frac{\text{RDI}_{\text{final}} - \text{RDI}_{\text{initial}}}{\text{age}_{\text{final}}} \times \text{age} + \text{RDI}_{\text{initial}}
\]

where \( \text{age} \) is the current age of the stand and \( \text{age}_{\text{final}} \) is the stand age at the end of the rotation. The RDI is allowed to vary around \( \text{RDI}_{\text{target}} \) within a constant interval determined by \( \text{RDI}_{\text{final}} \); when \( \text{RDI} \) reaches \( \text{RDI}_{\text{target}} \times (1 + \text{RDI}_l) \) the stand is thinned to \( \text{RDI}_{\text{target}} \times (1 - \text{RDI}_l) \) (RDI is fixed to 0.2 × \( \text{RDI}_{\text{target}} \), see Supplementary Data Fig. S1). Final commercial cutting occurs when the age of the stand reaches \( \text{age}_{\text{final}} \) or when the mean CBH of the stand rises above a given value.

The thinning-induced modification of the tree distribution is determined by a probabilistic harvest sub-module (Bellasen et al., 2010). In this approach, each tree is given a probability of cutting determined by \( P_{\text{min}}, P_{\text{max}} \) and \( T_{\text{strat}} \), corresponding to the minimum and maximum probabilities of cutting and the thinning strategy index, respectively. \( T_{\text{strat}} \) determines which CBH classes are to be preferentially thinned, allowing for a wide panel of silvicultural scenarios. After cutting, harvested volume is calculated and the thinning intensity (\( \tau_h \)) is determined as:

\[
\tau_h = \frac{\text{vol}_{\text{thin}}}{\text{vol}_{\text{tot}}}
\]

where \( \text{vol}_{\text{thin}} \) and \( \text{vol}_{\text{tot}} \) are the thinned volume and the total volume, respectively.

The harvest sub-module is fully described in the supplementary information.

Model structure: coupling methodology

The annual stand biomass increment prediction from CASTANEA is first converted to stand volume increment (see ‘Above ground volume calculation’ in the Supplementary Data) and then used as an input in the SSM, where it is disaggregated among a distribution of individual trees (Fig. 1). To ensure consistency between individual tree growth and stand volume increment, \( \sigma_{\text{aim}} \) and \( \gamma_{\text{aim}} \) [from eqn (1)] are annually adjusted (see ‘Modelling of the changes in stand structure’ in the Supplementary Data) so that the sum of the individual volume increment (calculated from basal area increments and initial CBHs) matches the stand-level prediction.

At each occurrence of a thinning event, changes in LAI are carried out in CASTANEA for the next simulation (Fig. 1). Biomass stocks are reduced by 100 \( \tau_b \) % [see eqn (6)]. \( \text{LAI}_{\text{target}} \) for a given year, \( y \), is determined by the following equation (see ‘CASTANEA: inter-annual variation of LAI’ in the Supplementary Data):

\[
\text{LAI}_{\text{thin}}(y) = \frac{\text{LAI}_{\text{max}}(y)}{a_{\text{LAI}} + b_{\text{LAI}} 100 \tau_h}
\]

where \( \text{LAI}_{\text{max}} \) and \( \text{LAI}_{\text{thin}} \) are the potential stand \( \text{LAI}_{\text{max}} \) and the actual stand \( \text{LAI}_{\text{max}} \) after thinning, respectively. \( a_{\text{LAI}} \) and \( b_{\text{LAI}} \) are species-specific parameters (Table 1).

CASTANEA-SSM allows for different scenarios of biomass exportation following thinning. The non-exported biomass goes to the litter compartment.

Study sites and field measurements

Long-term growth and physiological data were obtained from the French permanent plot network for the monitoring of the forest ecosystem (RENCEFFOREST, which is part of the ICP Forest Level II program; Ulrich, 1997). The data set included measurements from 14 forest sites of common beech and 18 forest sites of temperate oak species (16 and two \( Q. \) petraea and \( Q. \) robur forest sites, respectively) distributed over mainland France (Fig. 2). Plots were set up in even-aged mature forest stands.

Growth measurements consisted of (1) dendrochronological sampling: in 1995, 30 overstorey trees per plots were cored to the pith at breast height with an incremental borer (Lebourgeois, 1997). The tree CBHs were also measured. Dendrochronological series were processed with standard methods, tree ring width was precisely measured and the series were dated (Lebourgeois et al., 2005; Mérian et al., 2011). (2) Forest inventories: from 1991 to 2009, extensive CBH surveys were regularly conducted on 0.5 ha in the central part of the plots (Cluzeau et al., 1998), for which thinning events (typically occurring
every 8 years) were reported. In a few cases (approx. 15 %), unreported thinning could strongly modify the dendrometric characteristics of the plots between two surveys; for this reason, we discarded survey findings displaying a stem number decrease <2 % per year. The data set finally included 2–5 surveys per plots (Supplementary Data Table S6), with time intervals between two measurements ranging from 2 to 5 years.

Other reported site characteristics were site index (calculated from dominant height measurements; Skovsgaard and Vanclay, 2008; Supplementary Data Table S6), soil water-holding capacity, LAImax and leaf nitrogen content (LNC). Soil water-holding capacity was estimated from soil depth and texture

changes in bark thickness (Dhôte and Hatsch, 2000). The annual size asymmetry of the growth (i.e. the ability of larger trees to have a higher growth rate than smaller trees) was then evaluated from 1995 backward, using the slope (hereafter $\gamma_{\text{data}}$) of a simple linear regression fitted to the 30 calculated CGH, and their corresponding BAI. This relationship has been reported to be positive and linear in beech and oak overstorey trees grown in even-aged high stands (Dhôte, 1999; Deleuze et al., 2004; Supplementary Data Fig. S8A, B), with non-zero BAI's above a positive CBH threshold (hereafter $\alpha_{\text{data}}$).

We investigated the species-specific dependencies of $\gamma_{\text{data}}$ and $\alpha_{\text{data}}$ using both productivity and stand structure variables within the linear mixed model framework. The intraplot correlation among observations was considered by including a temporal covariance structure in the residuals, using a first-order autoregressive model [eqn (9)]. The autocorrelation parameter ($\rho$) was estimated jointly with the other parameters. The spatial and temporal variability of $\gamma_{\text{data}}$ and $\alpha_{\text{data}}$ were addressed by conducting analyses on both raw data and within-plot standardized data. The terms included in the final model were as follows:

(1) Species ($k$, unitless, a factor)
(2) Site index ($SI$, m, a covariate): used as a proxy for the site productivity
(3) Annual productivity ($AP$, mm2, a covariate): defined as the annual mean BAI of the cored trees, used as a proxy for the interannual variation of the productivity within a given site
(4) Maximum CBH ($CBH_{\text{max}}$, cm, a covariate): defined as the mean CBH of the five largest sampled trees, used as a proxy for the dendrometric features of the stands
(5) $\gamma_{\text{data}}$ or $\alpha_{\text{data}}$ (mm2 cm$^{-1}$ or cm, respectively, covariates): used to test the significance of the dependency between the two stand structure variables

Overall models could be written as follows:

$$
\begin{align*}
\gamma_{\text{data},i,k} &= a + \alpha_k + (b + b_k)\sigma_{\text{data},i,j} + (c + e_k)SI_j \\
\sigma_{\text{data},i,k} &= a + \alpha_k + b + b_k\gamma_{\text{data},i,j} + (c + e_k)SI_j \\
&+ (d + d_k)AP_{i,j} + (e + e_k)CBH_{\text{max},i,j} + E_{i,j,k}
\end{align*}
$$

where $i$, $j$, and $k$ are year, plot and species, respectively.

![Figure 2](http://aob.oxfordjournals.org/) Location and altitude of the RENECOFOR plots.
\[ \text{Var}(E_{i,j,k}) = \sigma^2 \]

\[ \text{corr}(E_{i,j,k}, E_{i,j',k'}) = \begin{cases} 
\rho^{||i-j||}, & \text{if } j = j' \text{ and } k = k' \\
0, & \text{otherwise}
\end{cases} \]  

The uncertainty in the \( \gamma_{\text{data}} \) and \( \sigma_{\text{data}} \) estimations varied strongly among years (Supplementary Data Fig. S8C, D). This uncertainty was considered in the analysis using a bootstrap procedure (Chernick, 2011). Models (8) were fitted 1000 times, randomly sampling at each iteration \( \gamma_{\text{data}} \) and \( \sigma_{\text{data}} \) values within their 95% confidence intervals. Only parameters with estimate distributions excluding zero values in a bilateral 5% probability level were retained. Analyses were conducted with the lme function of the package nlme in the R software (R Development Core Team, 2013).

Model parameterization

The PBM CASTANEA includes site-specific parameters (Supplementary Data Table S6) and an important number of species-specific parameters (Le Maire et al., 2005; Davi et al., 2005; Dufresne et al., 2005; see ‘CASTANEA: species-specific parameterization’ in the Supplementary Data). The parameters of the SSM are provided in Table 1. In particular, parameterization of the individual tree growth model [eqn (1)] has been based on the analysis of the growth size asymmetry over the RENECOFOR network. Indeed, eqn (1) and the growth size asymmetry analysis both relied on the same relationship between tree CBH and tree BAI (see ‘Size asymmetry of growth’ section and Fig. 1). For this reason, \( \sigma_{\text{sim}} \) and \( \gamma_{\text{sim}} \) were parameterized based on \( \sigma_{\text{data}} \) and \( \gamma_{\text{data}} \) dependencies, respectively.

Model evaluation

The fully coupled CASTANEA–SSM model was evaluated against forest inventories over the period from 1991 to 2009 (this data set was not used in the model calibration; see Model structure sections). Forest inventories conducted in 1991 were used to initialize (1) stand biomass in CASTANEA and (2) tree size distribution in the SSM. LAI_{max} was initialized with the averaged value obtained from the litter collection. The SAFRAN database (Vidal et al., 2010) was used for half-hourly climatic forcing. The simulations also benefited from site-specific field measurements of leaf nitrogen content and soil water-holding capacity. We assessed the ability of CASTANEA–SSM to simulate the averaged basal area increment and the averaged mean CBH increment of beech and oak stands grown under contrasted conditions. The moderate Pearson correlations between these two observed variables (\( r = 0.58 \) and \( r = 0.51 \) for beech and oak, respectively) indicate that they provide complementary information on stand structure changes. Model performance was evaluated using the coefficient of determination of the model (\( R^2 \)), root mean square error (RMSE) and average bias (AB) (Vanclay and Skovsgaard, 1997).

### Table 2. Description of the simulated thinning treatments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Description</th>
<th>RDI\text{initial}</th>
<th>RDI\text{final}</th>
<th>N\text{initial}</th>
<th>N\text{final}</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>Natural self-thinning (control)</td>
<td>1</td>
<td>1</td>
<td>590</td>
<td>450</td>
</tr>
<tr>
<td>T1</td>
<td>Commercial thinning: low intensity</td>
<td>0.9</td>
<td>0.7</td>
<td>590</td>
<td>60</td>
</tr>
<tr>
<td>T2</td>
<td>Commercial thinning: intermediate intensity</td>
<td>0.9</td>
<td>0.55</td>
<td>590</td>
<td>60</td>
</tr>
<tr>
<td>T3</td>
<td>Commercial thinning: high intensity</td>
<td>0.7</td>
<td>0.4</td>
<td>590</td>
<td>45</td>
</tr>
</tbody>
</table>

RDI\text{initial} and N\text{initial} are RDI and stem number per hectare at the beginning of the simulation (age = 40); RDI\text{final} and N\text{final} are RDI and stem number per hectare at the end of the forest rotation (age = 150). N\text{final} are approximate values.

Assessing management effect on forest functioning at the France scale

We run CASTANEA–SSM over metropolitan France with an 8 km resolution, using the SAFRAN grid for climate inputs (1989–2009 period, looped six times) and soil parameters from the French soil database aggregated to 8 km resolution to provide spatialized soil water-holding capacity (Cheaib et al., 2012, Supplementary Data Fig. S2). All grid points were initialized with a given tree size inventory and leaf nitrogen content and run over 110 years (stand ageing from 40 to 150 years) and 70 years (stands ageing from 40 to 110 years) for oak and beech, respectively. Four simulations were run with contrasted parameterization of the SSM (Table 2), corresponding to contrasted thinning intensities: a control treatment (C) and three treatments of increasing thinning intensity (T1–T3). The highest thinning intensity goes beyond the current guidelines (approx. 70 stems are currently recommended at the end of the forest rotation; Bock et al., 2007; Sardin, 2008). We assessed the influence of thinning on C fluxes [gross primary productivity (GPP)], total autotrophic respiration (R_{\text{tot}}) and net primary productivity (NPP) and growth [above-ground biomass increment (AGBI)] averaged over the forest rotation. We additionally analysed the distribution of average AGBI values over the territory.

We restricted our analysis to the grid cells where the species presence had effectively been observed (IFN, France, http://inventaire-forestier.ign.fr/spip/) and where CASTANEA predicted no partial or complete mortality event (i.e. not at the species distribution margins, representing >90% of the IFN grid cells): 2951 and 5403 grid cells were retained for beech and oak, respectively.

**RESULTS**

**Variation of the mode of competition**

We observed a significant positive correlation between the size-asymmetry index \( \gamma_{\text{data}} \) and productivity for both species (Supplementary Data Table S7): (1) across stands, with \( \gamma_{\text{data}} \) being greater on sites with high productivity (estimated through the site index, Fig. 3A, C); and (2) within stands, temporal variations of \( \gamma_{\text{data}} \) were linked to the interannual variability of productivity (Fig. 4A, B). Slopes of the \( \gamma_{\text{data}} \)-productivity
relationship differed significantly between oak and beech at both scales (Supplementary Data Table S7).

On the other hand, the circumference (CBH) threshold for significant growth $\sigma_{\text{data}}$ was found to be only related to the maximum CBH of cored trees (CBH$_{\text{max}}$), with non-different slopes across species at both spatial (Fig. 3B, D) and temporal (Supplementary Data Fig. S7A, B) scales.

There was no significant dependency between $\sigma_{\text{data}}$ and $\gamma_{\text{data}}$ (Supplementary Data Table S7).

Modelling of the changes in stand structure

The SSM parameterization aimed at reproducing the spatial and temporal dynamic of the mode of competition, which determines the evolution of the stand structure. Consequently, $\sigma_{\text{sim}}$ was first calculated using the $\sigma_{\text{data}}$–CBH$_{\text{max}}$ dependency (Fig. 3B–D). The $\gamma_{\text{sim}}$ value was then adjusted so that the sum of the tree volume increments matched the CASTANEA stand-level prediction. High stand-level productivity thus meant more size-asymmetric simulated growth.

Performance of the fully coupled CASTANEA–SSM model

As a prerequisite result, CASTANEA calibrated over the 1970–1990 period was able to simulate the averaged stand volume increments ($R^2 = 0.79$ and $R^2 = 0.87$ for beech and oak, respectively; data not shown). Further, the fully coupled CASTANEA–SSM efficiently predicted the changes in average temporal stand structure from 1991 to 2009, assessed through stand basal area (Fig. 5A–C) and mean stand CBH (Fig. 5B–D) increments, with $R^2 > 0.8$. CASTANEA–SSM predicted well the structure changes of stands with contrasted productivities, reflecting a large panel of environmental conditions (Fig. 5). No significant average bias was found in the prediction of both variables (i.e. the 1 : 1 line of a given plot is included in the 95% confidence interval of the fitted regression line).

![Fig. 3. Significant dependencies of $\gamma_{\text{data}}$ and $\sigma_{\text{data}}$ at the spatial scale for beech (A, B) and oak (C, D). Red lines are regression fits, dotted lines are 95% prediction intervals, coloured areas are 95% confidence intervals for beech (green) and oak (blue).](http://aob.oxfordjournals.org/)

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We observed that thinning in AGBI was low and comparable between beech and oak which led to a slight increase in the AGBI (Fig. 6C). This increase appeared to be consistent, we only drew a comparison.

Increasing intensity of thinning had a quasi-linear effect on on LAImax was related to the frequency and the intensity of the silvicultural operations (Fig. 8), but also to average annual water stress (Supplementary Data Fig S1), which determine the LAImax post-thinning resilience (i.e. the time needed to recover initial LAImax, Fig. 8). The thinning-induced drop in average LAImax was strongly related to an alleviation of water stress over the forest rotation (Supplementary Data Fig. S11).

Overall, the grid cells could be pooled in three distinct categories (Fig. 7), as follows.

1. Cells with a moderate thinning effect ($<4\%$) and high growth ($>180$ g C m$^{-2}$ year$^{-1}$). These cells where characterized by optimal conditions for growth, especially low water stress. Consequently LAImax recovered quickly after cutting (Fig. 8) and the thinning effect on growth was moderate.

2. Cells with a moderate thinning effect ($<4\%$) and low growth ($<180$ g C m$^{-2}$ year$^{-1}$). In these cells, little thinning occurred (Fig. 8) because growth was strongly limited by different environmental factors (e.g. high water stress, low temperature or low radiation, which limit photosynthesis and growth). Thinning-induced effects on growth were thus limited. This group also includes cells where LAImax decreased in response to a lack of carbohydrate reserves, reducing the relative impact of thinning.

3. Cells with a high thinning effect ($>4\%$). In these cells, growth was high enough to trigger a regular thinning (due to a rapid RDI increase; Supplementary Data Fig. S1). The thinning effect on LAImax was important because of medium to high annual water stress, leading to low post-thinning resilience (Fig. 8).

Areas displaying a moderate influence of thinning are consequently primarily located at high elevation or at the southern edge of the species distribution (group 2; 20 and 14% of the territory for beech and oak, respectively), and in high forest productivity zones in northern and eastern France (group 1; 56 and 59% of the territory for beech and oak, respectively). Areas where the thinning effect was high (group 3; 24 and 27% of the territory for beech and oak, respectively) are located a low elevation plains (Fig. 2) where annual water stress is high (Fig. 7) because of high climatic water demand or low soil water-holding capacity (Supplementary Data Fig. S2).

**DISCUSSION**

We present a new functional–structural model allowing prediction of stand structure changes over forest rotation. Our model is built upon the coupling between the physiological knowledge...
provided by the CASTANEA model and an SSM based on an empirical relationship between individual tree size and growth. CASTANEA–SSM was successfully evaluated against averaged dendrometric variables from inventories of 20 years in deciduous forests throughout France. The ability of the model to reproduce the temporal evolution of the entire tree size distribution characteristics (e.g. size inequality and skewness) could not be evaluated in this restricted time period survey. However CASTANEA–SSM satisfactorily simulates the changes in general features expected in a tree size distribution across a temperate forest rotation (i.e. simulated coefficient of variation and skewness decrease with stand mean size; data not shown). The coupled CASTANEA–SSM model can be used to explore the effect of realistic and operational thinning strategies on stand functions, by simulating stand variables usually found in forest management (e.g. RDI, basal area). Further, the coupled model allows simulation of adaptive silviculture, with a thinning frequency function of the individual growth rate, in order to investigate the impact of climate change on wood supplies (Pussinen et al., 2009). Lastly, CASTANEA–SSM will be used to investigate the impact of fundamental competition rules (such as self-thinning; Caspersen et al., 2011) on long-term forest stand functioning, along with the size dependency of physiological processes (e.g. the effect of hydraulic conductance on stomatal control and growth), which has been reported as a major key challenge for physiological modelling (Poschenrieder et al., 2013).

In the following we discuss: (1) the rules of tree growth competition used in the SSM calibration; (2) the functional implications of thinning in terms of stand–atmosphere C fluxes and within-stand C allocation; and (3) the potential of management to affect forest functioning at the national scale.

![Graphs showing evaluation of the fully coupled CASTANEA–SSM on long-term stand structure data from forest inventories, for beech (A, B) and oak (C, D). Coloured areas are the 95% confidence interval of the fitted regression lines for beech (green) and oak (blue). AB, average bias; RMSE, root mean square error.](http://aob.oxfordjournals.org/)

**Fig. 5.** Evaluation of the fully coupled CASTANEA–SSM on long-term stand structure data from forest inventories, for beech (A, B) and oak (C, D). Coloured areas are the 95% confidence interval of the fitted regression lines for beech (green) and oak (blue). AB, average bias; RMSE, root mean square error.
The rules of tree growth competition in beech and oak temperate forest

The SSM is based on the widely acknowledged relationship between tree size and growth (Coomes et al., 2011). Size–growth relationship prediction indeed allows determination of the changes over time of an initial tree size distribution and is therefore related to changes in size inequality and stand structure. The annual size–growth relationship was assumed to be a simple regression line between tree circumference (CBH) and tree basal area increment (BAI). The two parameters of the size–growth relationship, namely the slope and the circumference threshold for significant growth, provided complementary information on tree competition rules.

On the one hand, we found a positive and significant relationship between the size asymmetry of growth (assessed through the slope parameter \( \gamma_{data} \)) and the stand productivity at both temporal and spatial scales and for both species (Figs 3 and 4). This result is in line with the findings of Pretzsch and Biber (2010) and Pretzsch and Dieler (2010), and confirms that increasing fertility, related either to among-site differences or to interannual climatic variations, induces a transition in the competition among trees from size symmetric to size asymmetric. This finding is consistent with the premise that under favourable growth conditions, the disproportional advantage of large trees in the competition for light leads to size asymmetry of growth. Conversely, under adverse conditions (i.e. under water or nutrient limitations of growth), competition is thought to be more size symmetric. We additionally reported that growth size asymmetry increased more rapidly with productivity for beech than for oak at both temporal and spatial scales. Beech is indeed more shade tolerant than oak (VonLüpke, 1998), meaning that small beech trees can grow and survive in the stand understory. Consequently, the canopy structures of beech stands are expected to be more heterogeneous, leading to more size-related competition for light when below-ground resources are not limiting. However, we must acknowledge that using growth as a proxy for competition-mediated resource distribution can be misleading (Weiner and Damgaard, 2006), for instance in the case of a strong size effect on the resource use efficiency.

On the other hand, we found no dependencies between productivity and the CBH threshold (parameter \( \sigma_{data} \)) Supplementary Data Table S7). A shift in this threshold corresponds to an equal BAI fluctuation in all the growing trees; for this reason, this result indicates that there was no higher sensitivity of smaller trees to the variability of the growth conditions. This finding is in line with the conclusions of Mérian and Lebourgeois (2011) and contradicts evidence that smaller trees experience greater water stress because of greater below-ground competition in beech and oak temperate forests (Jacquart et al., 1992; Kloeppel et al., 1993; see also De Luis et al., 2009 for Pinus sp.). Rather, we found that the CBH threshold \( \sigma_{data} \) was significantly related to the CBH of the largest sampled trees at both temporal and spatial scales, with a similar slope for beech and oak (Fig. 3; Supplementary Data Table S7). This dependency could be due to the shift toward higher CBH of the growing tree distribution as the stand ages: CBH trajectories of the smallest trees with non-zero growth are strongly correlated with those of the largest trees in even-aged beech and oak stands (Dhoˆte, 1999). We consequently highlighted a monotonous change with stand age of the CBH threshold for significant growth, which is not influenced by the environmental factors causing growth to vary and indicates a conservative size hierarchy in beech and oak stands. Further, these results indicate that tree growth competition in deciduous mature temperate forest can be represented without the spatially explicit framework that strongly limits the potential applications of most tree-level growth models (Poschenrieder et al., 2013).

The functional implications of thinning

A coupled process-based–empirical modelling of the size–growth relationship fluctuations successfully reproduced the effects of environmental factors and tree-to-tree competition on average stand structure changes across a wide ecological
gradient. We were consequently able to quantify the influence of thinning on forest C fluxes and growth over France, to highlight the potential of management to affect forest functioning. We compared the effects of contrasted management regimes: a control treatment where only self-thinning occurs and three contrasted thinning intensity treatments. Increasing thinning intensity led to an increase in NPP which was the result of two different effects of thinning (Fig. 6), a slight decrease in GPP and a stronger decrease in \( R_{tot} \). The important negative thinning effect on \( R_{tot} \) is tightly linked to the reduction of the living stand biomass. This is realistic as the maintenance respiration of the above-ground woody biomass (stem and branches) represents about one-third of the total C lost by the ecosystem in a beech forest (Granier et al., 2000; Damesin et al., 2002). Moreover, CASTANEA is able to reproduce this proportion of ecosystem C losses efficiently (Davi et al., 2005). Conversely, the reduction in annual LAI\(_{\text{max}}\) following thinning had little average impact on GPP whatever the thinning intensity (Figs 6 and 8). This result, in line with the report from Grote et al. (2011), is primarily due to the asymptotic relationship between LAI\(_{\text{max}}\) and GPP (LeMaire, 2005), which is a direct consequence of both the exponential decrease of visible light interception (Monsi and Saeki, 2005) and photosynthetic capacity (Ellsworth and Reich, 1993) in the canopy.

Further, we observed that thinning-induced LAI\(_{\text{max}}\) reduction could significantly alleviate the average stand water stress (maximum approx. \(-10\%\); Supplementary Data Fig. S11) by reducing canopy transpiration. The incident global radiation, strongly linked to the canopy transpiration (Monteith, 1981), is indeed moderately attenuated when going from the top to the bottom of the canopy (Baldocchi et al., 1984). As a consequence, transpiration occurs in all the canopy layers and a decrease in LAI\(_{\text{max}}\) leads to a decrease in canopy transpiration even if the LAI\(_{\text{max}}\) remains at high values (LAI\(_{\text{max}}\).4; Fig. 8). This thinning-induced water stress alleviation has positive effects on stomatal conductance and C assimilation, and is therefore another factor reducing the detrimental effect of canopy reduction on GPP. In line with these results, LAI reduction has been shown to be an important process in the long-term forest acclimation to drought (Martin-StPaul et al., 2013). A positive effect of thinning on stand water relations has been assessed for a long time in field experiment (e.g. Bréda et al., 1995; Rodríguez-Calcerrada et al., 2011) but still had to be incorporated within stand growth PBMs to quantify the intensity and duration of thinning effects on fundamental processes and define future adaptive guideline.

On first exposure, the positive effect of thinning on NPP and AGBI conflicts with an empirical rule widely use in forest
cannot be used to predict the functioning of open-grown trees, with our results (Zeide, 2001; Skovsgaard and Vanclay, 2008). Indeed, one should note that the generality of the Eichhorn rule is still under debate; other relationships are suggested that imply an optimal thinning intensity for stand growth, in line with our results (Zeide, 2001; Skovsgaard and Vanclay, 2008). On the other hand, the limits of our modelling approach have to be considered. The simulated canopy of the CASTANEA PBM cannot be used to predict the functioning of open-grown trees, so we restricted our analysis to closed-canopy silvicultural guidelines (around 45 stems at the end of a forest rotation in the T3 treatment). This can explain that we did not report an important GPP drop when simulating heavy thinning treatment. Besides, CASTANEA—SSM did not include allometric scaling laws that could have resulted from natural selection-driven vascular network optimality: under this hypothesis, vascular networks minimize hydrodynamic resistance while maximizing resource uptake, which set allometric constraints in plant development (Enquist, 2002). These allometric constraints could put a physical limit on the potential growth of trees and thus on the stand growth capacity under low stem number—heavy thinning treatment (the maximum simulated CBH at the end of the forest rotation was approx. 3.5 m in our modelling exercise).

Most importantly, we observed that the amplitude of growth change was weak, especially compared with biomass estimation uncertainty (Lecointe et al., 2006), which makes it difficult to assess in the field. A major reason for this low absolute effect of thinning is the changes in average C allocation. Our simulations revealed that the extra C assimilated after thinning is predominantly attributed to the fine root compartment (Supplementary Data Fig. S9), following allocation equilibrium rules between leaf, fine root and carbohydrate reserve implemented in CASTANEA (Davi et al., 2009). The maintenance respiration C cost of fine roots is high (Ryan et al., 1996; Epron et al., 1999) and consequently limits the decrease of total respiration — and the associated increase in NPP and AGBI — following stand woody biomass reduction. This finding is in line with field experiments reporting enhanced biomass and turnover of fine roots after thinning (Santantonio and Santantonio, 1987; López et al., 2003). Our modelling approach thus suggests that changes in C allocation are a plausible physiology-based explanation of the empirical Eichhorn rule.

**The potential of management to affect forest functioning at the national scale**

Our simulations clearly indicated an enhancement of net C assimilation and growth in managed forests. This positive thinning effect appeared to be different over the territory for the two species. We showed that the intensity and frequency of thinning strongly interact with LAI\textsubscript{max} resilience in determining the thinning effect on growth (Fig. 8). The management effects appear to be more contrasted over France for the oak stand (Fig. 7), mainly because LAI\textsubscript{max} resilience is lower and thinning therefore has a longer effect on forest functioning (see ‘CASTANEA: interannual variation of LAI\textsubscript{max},’ in the Supplementary Data). Under the hypothesis of forest management for commercial purposes, the intensity and frequency of thinning are determined by the forest productivity: the higher the growth, the more frequently silvicultural operations are required to keep the stand within the guideline boundaries. This partially explains the low thinning effect on low growth stands, so this result could be different, for example, in the case of high thinning intensity to maintain relict stands at the edge of the species distribution (Pérez-de-Lis et al., 2011). The highest thinning effect was reached in a zone with regular thinning interventions and low LAI\textsubscript{max} resilience due to moderate to high water stress (corresponding to forest with

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**FIG. 8.** Simulated temporal dynamics of stand biomass (A), LAI\textsubscript{max} (B) and gross primary productivity (C) over a forest rotation for oak stands. Filled symbols indicate year of thinning.
current intermediate productivity). Interestingly, these zones will be the first production forests impacted by the increase of drought intensity and frequency mediated by climate change.

**Conclusions**

Our modelling approach consequently could help in identifying the proportion of the territory where management efforts should be concentrated to mitigate near-future drought impact on national forest productivity. Around a quarter of the French temperate oak and beech forests are currently in zones of high management potential and high climate change vulnerability. This proportion could increase rapidly if increasing water stress affects non-limited high growth stands. Process-based models incorporating stand structure modelling can be used to define physiology-based adaptive management prescriptions (Pussinen et al., 2009): our findings indicate that heavy thinning beyond the current guidelines (approx. 50 stems at the end of the forest rotation) could profitably be tested without productivity loss.

**SUPPLEMENTARY DATA**

Supplementary data are available online at www.aob.oxfordjournals.org and provide details of the following. 1. Simulated features over forest rotation of a stand under thinning treatment. 2. Spatialized soil parameter. 3. Above ground volume calculation. 4. SSM: harvest sub-model. 5. CASTANEA: soil water stress index. 6. CASTANEA: inter-annual variation of LAI\textsubscript{max}. 7. CASTANEA: inter-annual variation of wood growth. 8. CASTANEA: species-specific parametrization. 9. Description of the RENOECOFOR sites characteristics. 10. Variation of the mode of competition. 11. Goodness of fit of the individual tree growth model. 12. Effect of contrasted thinning treatments on average annual C allocation. 13. Thinning effect assessment on AGBI distribution.

**ACKNOWLEDGEMENTS**

We wish to thank the Office National des Forêts and the RENOECOFOR network team, particularly Marc Lanier, for providing us with the database. The SAFRAN database was provided by Météo-France as part of the HYMEX project. J.G. receives a PhD grant from the French Ministère de l’Enseignement Supérieur et de la Recherche and the University of Paris Sud. A post-doctoral research grant to N.K.M.-S. was provided by the Humbolt project within the GIS climat.

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